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Fossil Mammals of Africa

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THE MIOCENE HYRACOIDS
OF EAST AFRICA

WITH SOME OBSERVATIONS ON THE ORDER HYRACOIDEA

BY

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THE MIOCENE HYRACOIDS OF EAST AFRICA

By T. WHITWORTH

I. INTRODUCTION

This monograph deals primarily with the Miocene hyracoids of the Kavirondo region of western Kenya (Text-fig. 1). The most important source of these fossils is Rusinga Island, which lies in the north-east corner of Lake Victoria Nyanza, at the entrance to the Kavirondo Gulf. The surface features of Rusinga Island are



FIG. 1. Regional map of part of East Africa showing the fossiliferous areas.

indicated in Text-fig. 2. The relief is provided by a series of flat-topped ridges and tables, capped by resistant agglomerate or lava. Lunene, the highest of these, rises over 1000 ft. above lake level. The drainage consists of temporary radial systems, arranged about the areas of higher relief. The deep gullies cut in the softer sediments along these drainage channels often provide rich fossil localities.

Detailed geological information concerning Rusinga Island is given by Kent (1944) and Shackleton (1951). The stratigraphical sequences established in Rusinga by these authors are as follows.

KENT	SHACKLETON
Lava cap : at least 300 ft.	Lunene lavas.
Upper agglomerate : up to 400 ft.	Kiangata agglomerate.
Tuffaceous Series : 40 ft.	Kathwanga and Kulu Series : variable thickness.
Argillaceous Series : variable thickness.	Upper Hiwegi Beds.
Basal agglomerate.	Lower Hiwegi Beds.
	Rusinga agglomerate group : up to 140 ft.
	Kiahhera Series : up to 350 ft.

It is generally agreed that all these deposits are of early Miocene age.

Kent includes the Kathwanga and Kiahhera Series in his tuffaceous and argillaceous groups. There can be little doubt, however, that his basal agglomerate is underlain by a thick sequence of older ashes, blocky tuffs and red earths. In addition the grey flags, mudstones and tuffs of the Kathwanga Series are appreciably younger than his Tuffaceous Series. The agglomerates consist of interbedded tuffs and massive nephelinite-agglomerate, that of the lower group being characterised by numerous melanite insets. The capping lavas are nepheline basalts, with phenocrysts of olivine and augite. The Hiwegi Beds are predominantly tuffaceous, with interbedded red argillaceous bands, and some thin red limestones. The Miocene beds of Rusinga Island thicken towards the south and south-west, with an increase and coarsening of their pyroclastic content, which probably indicates a source in the Kisingiri volcanic centre. The general facies of the beds suggests that their accumulation was fairly rapid. The geological structure is simple ; most beds are nearly horizontal and cut by a few normal faults. The vertebrate fauna is distributed throughout almost the entire bedded sequence, but is most profusely represented in the Hiwegi Beds, Kathwanga-type sediments and the red earths of the Kiahhera Series.

The Rusinga deposits are usually regarded as lacustrine sediments, accumulated in a shallow basin, which occupied part of the present Kavirondo Rift. It is possible, however, that the deposits were to a large extent subaerial, or were laid down in the ephemeral lakes and on the floodplains of a semi-arid region of indeterminate relief. Only in Kathwanga times do fairly extensive and permanent lake conditions seem to have been established (Whitworth, 1953).

In addition to Rusinga Island, other localities from which hyracoid remains have been collected are : Maboko Island, Mfwanganu Island, Karungu and Songhor (Text-fig. 1). Kent states that the Miocene sequence at Mfwanganu closely parallels that of Rusinga. The stratigraphical sequences at Songhor and Maboko are also

described by Kent (1944), and the sequence at Karungu by Oswald (1914). At Maboko exact dating of the sediments is complicated by the possibility of a mixed fauna, and Hopwood (in discussion on Shackleton, 1951) suggested that, on the evidence of the proboscideans, the assemblage may be divisible into two.



FIG. 2. Map of Rusinga Island indicating the surface relief and showing the fossiliferous localities.

For the composition of the mammalian faunas of these Miocene deposits, reference may be made to the summary drawn up by Le Gros Clark & Leakey (1951 : 5).

The fossiliferous sites on Rusinga Island, from which mammalian remains have

been recovered, are at present numbered from R.1 to R.113. The location of these sites is indicated in Text-fig. 2. They are classified provisionally as follows :

R.1	Lower Hiwegi Beds
R.1a	" "
R.2	Kulu Series
R.3	Upper Hiwegi Beds
R.4	Kulu Series
R.5	Red band in upper part of Kathwanga Series
R.10-19	Lower Hiwegi Beds
R.20-29	Kulu Series
R.30-40	Upper part of Kathwanga Series
R.71	?Lower Hiwegi Beds
R.73	Kiahera Series
R.74-75	Kiahera Series
R.76	?Kiahera Series
R.80-99	Lower part of Kathwanga Series
R.100-112	Lower part of Kathwanga Series or Kiahera Series
R.113	Kiahera Series
Sienga-Lunene ridge	Kiangata agglomerate
East of Utaju	Upper Hiwegi Beds
Wakundu	Kulu Series
Wanyama	Lower Hiwegi Beds
Kalim	Kiahera Series

Of the material described in this paper, those specimens with a registration number prefixed by the initial M. are in the Department of Geology, British Museum (Natural History). All other material is at present in the Coryndon Museum, Nairobi.

II. HISTORY OF RESEARCH INTO FOSSIL HYRACOIDS

The first fossil hyracoid was discovered by Gaudry in the Pontian bone beds of Pikermi, near Athens, during his excavations in 1855 and 1860. The material, consisting of the right and left halves of an adult mandible, was subsequently described (Gaudry, 1862) under the name *Leptodon graecus*, and classed as "Rhino-ceride du groupe des Palaeotherium".

A similar Pontian fauna was later discovered on the island of Samos, but it was not until 1899 that Osborn described a skull from Samos, which he called *Pliohyrax kruppi*. In the same year Schlosser described a mandible of *Pliohyrax* from Samos, and established its identity with Gaudry's mandible from Pikermi. Forsyth-Major (1899) then pointed out that the name *Leptodon* had been used in 1835 for a genus of birds, and that the valid name was *Pliohyrax* Osborn, the correct specific name being *P. graecus* (Gaudry).

In 1879 Schweinfurth discovered vertebrate-bearing marine and fluvio-marine deposits of lower Oligocene age in the Fayum depression, 70 miles south-west of Cairo. During the years 1901-04 Beadnell and Andrews collected numerous fossils, representative of all vertebrate classes except Amphibia, from these beds. Among them were included remains of hyracoids. In his catalogue of 1906, Andrews recognised two genera of hyracoids, *Saghatherium* and *Megalohyrax*, which he placed in the family Saghatheriidae. A third genus, *Geniohyus*, he erroneously regarded as an early pig, but later (1907) suggested that it might possibly be related to the Hyracoidea. In a revision of the Fayum vertebrates, Schlosser (1911) divided the hyracoids into six genera, *Megalohyrax*, *Saghatherium*, *Pachyhyrax*, *Mixohyrax*, *Bunohyrax* and *Geniohyus*, all grouped within the family Saghatheriidae.

In 1911 Oswald collected from freshwater beds at Karungu on the north-east shore of Lake Victoria, a rich variety of vertebrate remains, including mandibular fragments of a small, rodent-like creature, which Andrews (1914) described (despite its superficial dissimilarity to known hyracoids) as *Myohyrax oswaldi*, and assigned to a new family, the Myohyracidae. Andrews suggested an early Miocene age.

In 1921 Matsumoto demonstrated the identity of Andrews' genus *Megalohyrax* and Schlosser's *Mixohyrax*, and segregated the specimens described by Schlosser as *Megalohyrax* under the new generic name *Titanohyrax*. In a second publication (1926) Matsumoto divided the Hyracoidea into five families, Geniohyidae, Titanohyracidae, Pliohyracidae, Myohyracidae and Procaviidae.

During the early 1920's extensive field studies were carried out by a German party in the Diamond Fields of South-West Africa. Vertebrate remains were collected from fluvial or lacustrine deposits in the coastal region south of Lüderitz, to which Stromer (1926) assigned a lower Miocene age. Among these fossils he distinguished two species of *Myohyrax*, *M. oswaldi* and *M. doederleini*. He also described two new genera and species of hyracoid: *Prohyrax tertiarius*, a slightly hypsodont form of medium size, showing similarity to *Saghatherium*; and a small hypsodont form, *Protypotheroides beetzi*. Attention was drawn to certain similarities between *P. beetzi* and the South American typotheres. A third species of *Myohyrax*, *M. osborni*, collected from the same region, was described by Hopwood (1929) three years later.

In 1932, during an expedition to the Lower Omo Valley, Abyssinia, Arambourg collected vertebrate remains from grits and conglomerates at Mount Losodok on the south-west shores of Lake Rudolph, Kenya Colony. Included was a small fragment of a left mandibular ramus, which he named (1933) *Plioxyrax championi*.

In 1934 Broom described, as *Procavia antiqua*, an early Pleistocene form found at Taungs, Bechuanaland. Shaw (1937) has also described a fossil coney, *Procavia transvaalensis*, from the Quaternary bone breccias of Sterkfontein.

III. SYSTEMATIC DESCRIPTION

Family GENIOHYIDAE Matsumoto, 1926

Genus MEGALOHYRAX Andrews, 1903, emend.

(= *Mixohyrax* Schlosser, 1911)

Hyracoidea of medium to large size. Skull long, low; snout long, narrow; orbit commences above M^2/M^3 . Hard palate extends behind posterior molars. Mandible long, shallow, increasing uniformly in depth to the rear; inner surface of each ramus pierced by large sub-circular fenestra, giving entry to cavity within the ramus; symphysis long and shallow. Cheek teeth brachyodont, upper buno-selenolophodont, lower buno-selenodont. Upper series closed from C to M^3 , incisors separated by diastemata. I^1 recurved and tusk-like; in male sharp, strongly ridged anteriorly, in female shovel-tipped. I^{2-3} reduced, simple, blade-like teeth. Lower series closed from P_1 to M_3 . Posterior third lobe in M_3 . Incisors and canine separated by diastemata. C very small, with simple, leaf-like blade; in smaller species close to P_1 . I_1 procumbent, spatulate, with pectinate extremity. I_2 similar in female, tusk-like in adult male. I_3 much reduced or absent.

Megalohyrax championi (Arambourg), 1933, emend.

(Pls. 1-4, 5, figs. 1, 2; Text-figs. 3-8)

DIAGNOSIS.—A *Megalohyrax* of large size and cursorial habit. Orbit small, open posteriorly, skull roof smooth. Upper premolars rectangular, molars wider in front. P^1 to M^3 molariform. Strong mesostyle, strong W-shaped ectoloph P^2 to M^3 ; metaloph weak. I^{2-3} much reduced; I^3 probably absent in some individuals. Lower cheek teeth molariform P_2 to M_3 , with weak, variable metastylid. C usually absent; when present, separated from P_1 by short diastema. Milk molars very similar to corresponding premolars. First molar in wear before fall of deciduous teeth. Post-cranial skeleton similar to *Procavia*. Tarsus resembles that of *Equus*; navicular and external cuneiform occupy almost entire width of tarsus; third metatarsal enlarged, lateral metatarsals reduced.

DISTRIBUTION.—Type locality, Losodok, east shore of Lake Rudolph, Kenya Colony. The material dealt with here is chiefly from Rusinga Island, but a few specimens from Karungu and Mfwanganu Island are included.

HOLOTYPE.—Fragment of a left mandibular ramus with P_{3-4} , preserved in the Muséum National d'Histoire Naturelle, Paris.

The detailed description which follows takes into account more than 200 specimens, but is based in particular upon the following material:

M.16387 *Brit. Mus. Geol. Dept.*.—A well-preserved male skull, lacking the lower jaw; recovered near R.3, Rusinga.

Coryndon Museum, 350 '50.—An almost complete female skull with lower jaw from R.1A, Rusinga.

Coryndon Museum 334 '47.—A collection of limb bones from R.1, Rusinga.

General Description of the Skull

The long, low and narrow skull has a flattened zygomatic arch, and an orbit which lies well back behind a slender, elongate snout with projecting nasal bones. The cranium is relatively smaller than that of Recent species, and the general proportions of the skull are strikingly similar to those of *Megalohyrax niloticus* (Schlosser).

In the male the fronto-parietal region is flattened, or slightly concave, in contrast to the rounded upper surface of the female skull. This difference, exactly paralleled in *Procavia*, is caused by the stronger development of temporal and sagittal crests in the male. In both sexes the skull roof is smooth, and passes down on either side into a thick supraorbital process. At the posterior end of the skull roof, the short, robust sagittal crest is confluent with the temporal crests (Pl. 2, fig. 2). The occiput truncates the cranium behind; it slopes backwards at a marked angle from the foramen magnum, which lies below the sagittal crest. The foramen magnum faces obliquely downward at an angle of approximately 45 degrees to the horizontal and the large occipital condyles are strongly inflated (Pl. 2, fig. 1). The bases of stout paroccipital processes flank the occipital condyles, and are slightly anterior to them. Anterior to, and slightly outside the paroccipital process lies the somewhat angular tympanic bulla. No distinct mastoid process can be seen in either M.16387 or 350 '50.

The snout is perhaps narrower and less powerful in the female than in the male. There is a moderately large antorbital foramen, about 67 mm. in front of the anterior margin of the orbit in M.16387, and about 55 mm. in 350 '50 (Text-fig. 3a). Above and in front of the antorbital foramen is a large, deep, naso-maxillary or facial fossa. In M.16387 this lies about 73 mm. in front of the orbital margin, in 350 '50 about 60 mm. A similar fossa occurs in a specimen of *Megalohyrax pygmaeus* (A.M.14454), described and figured by Matsumoto (1926). This last specimen is probably the only skull of an Oligocene species of *Megalohyrax* in which the fossa is preserved.

In front of the orbit, the sides of the face are steeply inclined; and they are slightly concave behind the antorbital foramen. The posterior margin of the orbit is indicated by a strong postorbital process, arising from the upper edge of the zygomatic arch. The arch curves downward appreciably in its passage forward from squamosal to maxilla. The maximum height of the zygoma, at the postorbital process, is about 28 mm. in M.16387; the interorbital width about 44 mm. Viewed from the palatal surface, the anterior internal limit of the arch is approximately in line with the choanae.

The basioccipital and basisphenoid form a prominent, flask-shaped body, tapering forward from the anterior surface of the occipital condyles. Flanking this flask-shaped ridge in M.16387 is an irregular vacuity which probably represents the foramen lacerum medium and the opening of the Eustachian canal. The foramen ovale and foramen rotundum are well preserved (Pl. 1), as also are the foramen lacerum

posterius and condylar foramen. All these openings are placed exactly as in *Procavia*. The glenoid fossa is extended transversely.

The hard palate extends a short distance behind the third upper molar. Along its median line, the palate is deeply and broadly excavated, so that the upper cheek teeth are set on well-defined lateral shelves. In 350 '50 the incisive foramen of the left side lies about 11 mm. behind the anterior extremity of the premaxilla.

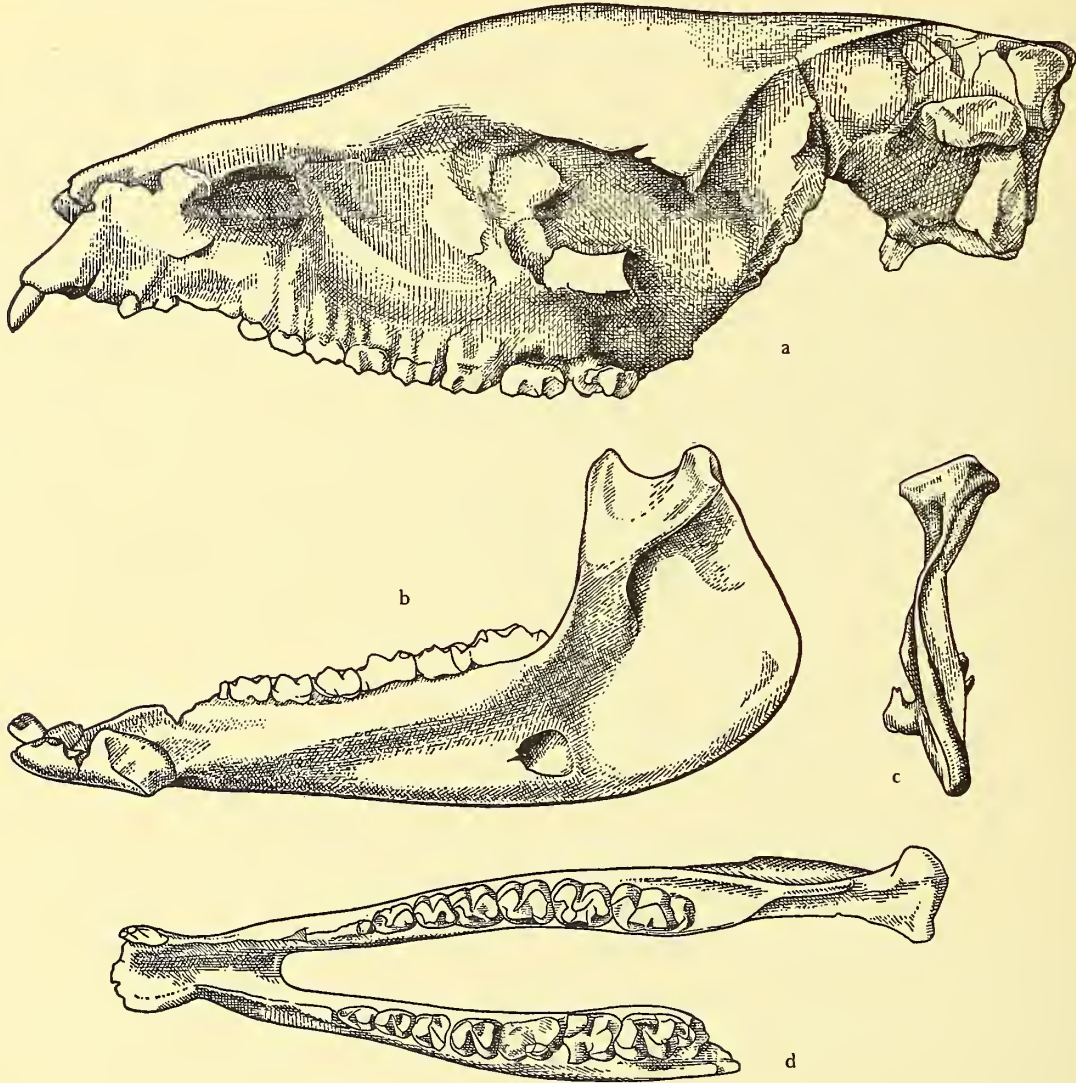


FIG. 3. Skull and lower jaw of an adult female of *Megalohyrax championi* (350 '50). (a) Lateral view of the skull, (b) internal view of the right mandibular ramus, (c) posterior view of the same, (d) occlusal aspect of the mandible. All $\times \frac{1}{2}$.

The mandibular rami are stoutly built, but are very shallow and elongate. Following a very slight concavity of the lower margin immediately behind the symphysis, the depth increases gradually and uniformly towards the rear. The grinding teeth form a closed series, convex labially, from first premolar to third molar. The symphysis is long and shallow; in 350 '50 it measures 43 mm. along the mid-line.

The rami, below the cheek teeth, are externally flattened and internally convex in front, becoming internally flattened and externally convex behind. In 350 '50 the mental foramen lies 14 mm. in front of the first premolar on the right side, and 12 mm. on the left side.

A striking feature of the mandible is the large fenestra, which penetrates the lingual surface of the jaw, and affords entry to a cavity within the body of each ramus. It is present in all adequately preserved material referred to this species, regardless of sex. Normally the fenestra lies below the third molar, and is usually situated 5 or 6 mm. above the inferior margin of the ramus. In most specimens it is oval, with the longer axis vertical (Pl. 4, fig. 1), although occasionally it is approximately circular. The dimensions vary between 12–20 mm. in vertical diameter and 12–17 mm. in horizontal diameter. The internal mandibular fenestra is particularly well preserved in 514 '48 (fragment of a left mandibular ramus with P_4 to M_3 from Wanyama, Rusinga, Pl. 3, fig. 3b). In this specimen it is of sub-circular outline, and the posterior ventral segment of the fenestral margin is slightly bevelled. The ventral border of the ramus, immediately behind the fenestra, is gently inflected to form a shallow, longitudinal channel, or fluting, confluent with the bevelling, and showing clear muscle imprints adjacent to the hinder margin of the fenestra.

The function of this relatively enormous fenestra is obscure. Except for the bevelling of its posterior margin, the fenestra penetrates the lingual wall of the ramus at right angles. In this respect it differs from normal foramina transmitting nerves and blood vessels, and may possibly have accommodated a muscular or glandular structure. It seems unlikely that it can be referred in any way to the mandibular foramen, which in other mammals, including the hyracoids, enters the mandible at a point behind the third molar. Schlosser (1911) suggested that the fenestra may have been associated with a persistent vestige of Meckel's cartilage. Perhaps an anterior slip of the pterygoid muscle extended forward along the channel at the rear of the fenestra, to obtain a tendinous insertion within the body of the ramus. This explanation is not altogether satisfactory, since there is no sign whatever of a muscle attachment within the cavity of the ramus; and it is difficult to visualise the mechanical advantage of such an attachment. For the moment it must be admitted that the purpose of the fenestra is unknown.

The anterior edge of the ascending ramus rises in a steep curve immediately behind the third molar. The edge is thickened internally and externally, the external thickening forming a prominent shelf outside M_3 . As in *Procavia*, these two thickenings enclose a lanceolate fossa in the anterior edge of the ramus, from which a canal leads back to its inner surface. The posterior opening of this canal lies in a deep, elongate fossa, which probably contains the mandibular foramen. The posterior fossa is bounded in front by a strong thickening, which curves back above the upper limit of the fossa to join the base of the condylar process. The position of this thickening is indicated externally by a shallow, complementary sulcation on the outer face of the ascending ramus. The semi-circular angle is thin and conchoidal, but possesses a thickened and slightly inflected lower rim. Generally speaking, the angle is broadly convex outside, and correspondingly concave within. The coronoid process is extremely small, and the articular condyle is greatly expanded transversely (Text-fig. 3c).

Fragments of three juvenile mandibles are included in the Rusinga collection. Two of these (C.M.Hy. 105 and 107, Pl. 3, fig. 4) are extremely small with dM_4 in process of eruption. The ramus is very shallow and broad to accommodate the relatively enormous cheek teeth, and although slightly flattened internally, is shaped like a boat. The ascending ramus arises on either side of the unerupted dM_4 . The angle is not well developed at this stage, since the inferior border of the ramus commences to rise beneath the rear face of dM_4 . A third specimen (C.M.Hy.62) is very slightly larger, and although thick in relation to its depth, approximates more closely to the proportions of an adult mandible. The internal mandibular fenestra is not preserved in this juvenile material.

TABLE I *
MEGALOHYRAX CHAMPIONI
Dimensions of Skull

	M.16387♂	350' 50♀	
Length of skull	277+	277	
Breadth of snout above M^1	80	76	
" at zygomata	116	102	
Height of skull from M^3 to frontal surface	80	77	
Ant. margin of orbit to ant. extremity	129+	139	
Supraorbital process to post extremity	104	99	
Horizontal diameter of orbit	44	39	
Vertical diameter of orbit	30	27.5	
Length of mandibular ramus	—	—	218
Height of ascending portion of ramus from coronoid to inferior margin	—	—	93
Depth of ramus in front of P_1	—	23	23
" " at rear of P_3	—	26	26
" " " M_2	—	35	37
Thickness of ramus below M_2	—	15	14.5

* In this and all subsequent tables, dimensions are always maxima and are recorded in millimetres. Where two figures are given, these refer to left and right sides, the left side being given first.

Upper Dentition

The upper cheek teeth are brachyodont, buno-selono-lophodont, and form a closed series of increasing size and complexity from the premolariform canine to the third molar. The dental arcade is very gently convex labially. Commencing with P^3 , the posterior teeth become increasingly trapezoidal, with the internal anterior angle posterior to the external anterior angle. The anterior margin is also broader than the posterior. These characters are caused by the strong development of the parastyle, and its incorporation in the crown proper. The effect is most marked in M^3 . All the cheek teeth except the canine are four-rooted. The upper incisors are separated from each other, and from the closed series of cheek teeth, by lengthy diastemata. I^{2-3} are much reduced, and the latter is often absent.

The upper molars are all very similar, and there is no development of a posterior third lobe in M^3 . The prominent, slightly compressed paracone and metacone are

the highest cusps of the crown. They are a little anterior to the protocone and hypocone, which are lower, stouter, and somewhat bunoid. On the outer side of the molars the powerful parastyle and mesostyle rival the paracone. The parastyle is in fact almost bunoid. The metastyle is somewhat weaker, but there is a pronounced hypostyle, which can be recognised in all teeth as far forward as P². Consequently the ectoloph possesses an angular, W-shaped outer wall. A protoloph joins the stout, bunoid protocone to a small, median-anterior protoconule. This crest occupies an oblique position, running forward from protocone to protoconule, and its trace is somewhat crescentic. The slightly smaller hypocone wears into a short, oblique metaloph. Sometimes a recognisable central metaconule is developed at its outer end. As wear progresses, the protoloph and metaloph both become confluent with the ectoloph. The order of coalescence is not regular. In the deep internal valley between the protocone and hypocone, the cingulum gives rise to a small accessory style. The cingulum is also well developed on the internal portion of the anterior face of the molars, where it runs diagonally up towards the protoconule, and often forms another small accessory style. Occasionally, similar styles may be developed on the external cingulum.

The second to fourth premolars are smaller replicas of the molars, although the hypocone is relatively reduced. This may simply mean reduced molarification, or



FIG. 4. Upper dentition of the left side, P¹ to M³, of *Megalohyrax championi* (91 '50), viewed from the occlusal aspect. Natural size.

may be partly due to crushing of anterior teeth as the posterior dentition is erupted. There is also a tendency to develop very small accessory styles on the external cingulum. The first premolar, however, is a small quadrangular tooth, in which the mesostyle is not developed. The metastyle is much reduced, and does not reach the occlusal surface: the parastyle forms a transversely compressed fold, projecting forward from the anterior external angle of the tooth. Consequently the outer wall of the ectoloph follows a gently undulating course. The canine is a blunt, roughly rectangular tooth, usually carried on three roots, and fitting closely against P¹. It is apparently premolariform, but in all available material is truncated by an inward-sloping, concave surface of wear, which prevents identification of individual cusps.

The first upper incisor of *Megalohyrax championi* exhibits a sexual dimorphism exactly paralleled in *Procavia*. In the female this tooth is large and somewhat pro-odont, roughly triangular in section, and with a shovel-like tip (Text-fig. 5a). The gently convex anterior face is the broadest, and the grooved median face the narrowest: the posterior or lingual face is of intermediate breadth, and slightly concave. The tooth lies with the median face in the sagittal plane of the skull. All surfaces of the terminal portion are covered by smooth enamel, which is thickest on the anterior surface. As wear proceeds the lingual surface of the tooth becomes cut by a concave occlusal surface, which is oblique to the long axis of the tooth, and at

right angles to the median plane of the skull. The tooth differs from the corresponding incisor of *Procavia* in its slightly more spatulate or shovel-like extremity, and in the greater lateral divergence of the tip. The terminal portion of the female incisor is sometimes notched at its external edge.

In the male the first upper incisor is tusk-like, recurved and sharply pointed (Text-fig. 5*b*). It is of pronounced triangular section, with the acute apical angle of the triangle forming a prominent anterior ridge. Of the two anterior faces, the broadly convex external face, lying parallel to the median plane of the skull, is the broader: the plane to convex internal face is the narrower. Both are covered by thick enamel. The posterior or lingual face of the tooth is strongly concave. Examination in ultra-violet light shows that there is a thin coating of enamel here, usually

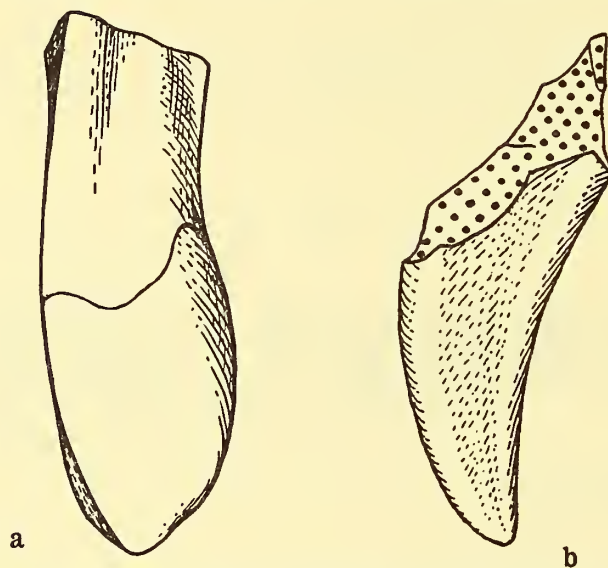


FIG. 5. Upper anterior incisors of *Megalohyrax championi*. (a) Antero-external aspect of the left I^1 of a female individual (C.M.Hy.14), (b) terminal portion of the left I^1 of a male individual (C.M.Hy.33) viewed from the external aspect. Both $\times 3$.

much reduced by wear. When a surface of wear is preserved on the lingual face, it is flat, and set at right angles to the sagittal plane of the skull.

The second upper incisor is a small, simple tooth, separated from I^1 by an appreciable diastema. In 350 '50 this diastema measures 20 mm., and the tooth lies 26 mm. in front of the canine. An isolated and well preserved tooth, from R.1, Rusinga (258 '50), is probably a second incisor; it is small, laterally compressed, and blade-like. Enamel is present on both faces of the erupted portion, but the proximal margin of the enamel becomes V-shaped towards the root on the labial face, and towards the extremity on the lingual. The length, including the root, is 16.7 mm., the maximum breadth across the labial face 4.2 mm., and the labio-lingual thickness 2.0 mm. The third upper incisor is only represented in one specimen, 264 '47 from R.3, Rusinga. Here the base of a very small, single-rooted tooth is preserved 10 mm. in front of the canine. The position is similar to that of the corresponding tooth in Schlosser's "*Mixohyrax*" *niloticus* (1911, pl. 15, fig. 8), but the tooth itself seems to

have been smaller than in Oligocene Megalohyraces. In all other adequate material from Rusinga, the third incisor appears to be suppressed.

A single specimen from R.1, Rusinga (C.M.Hy.7, Pl. 5, fig. 1) retains the second, third and fourth milk molars. It is part of a left maxilla with dM^2 to M^2 in a gently arched series, and C to P^4 visible within the crypts. M^2 is fully erupted and in wear. The deciduous molars, although badly worn, appear to be fully molariform. In crown pattern they are similar to the corresponding premolars, but may perhaps show a slightly better molarification. In common with the adjacent true molars, they have the internal cingulum strongly developed. In *Megalohyrax championi* the upper deciduous teeth were clearly not replaced until the first and second molars were in use. The third molar, however, was the last tooth to be erupted in the upper jaw.

Lower Dentition

The bunio-selenodont lower cheek teeth are brachyodont, and increase in size from P_1 to M_3 . The third molar, the largest tooth, possesses a pronounced third lobe, which is usually about 6–7 mm. in breadth. A single isolated third molar (C.M. Hy.74) has a much reduced and compressed third lobe, which measures only 3 mm.



FIG. 6. Lower dentition of the left side, P_2 to M_3 , of *Megalohyrax championi* (C.M.Hy.58), viewed from the occlusal aspect. Natural size.

across, but in all other respects conforms to the normal pattern. The third and fourth premolars are fully molariform, the second is perhaps slightly less so, and the first is clearly sub-molariform. All the teeth, except the first premolar and the five-rooted third molar, have four roots. The first premolar normally has three, two at the rear and one in front, but in two specimens (C.M.Hy. 106 and 1116) the anterior root is grooved and divides below the alveolar margin. The enamel of the lower cheek teeth usually shows a faint annular wrinkling.

The first and second lower incisors are large and closely approximated. In 350 '50 (female) and 1065 '50 (male) the diastema between I_2 and P_1 is about 45 mm. long. In most of the material it would seem that the lower canine and third incisor are completely suppressed, but the canine is represented in two specimens, and two isolated canines have been found on Rusinga. In 324 '47b the base of an anteriorly inclined canine may be seen 3 mm. in front of P_1 , and in C.M.Hy.59 there are signs of a tooth 2 mm. in front of P_1 . A similar restricted occurrence of the permanent canine was reported by Hahn (1934) in a species of *Procavia*. Although the canine is apparently absent in C.M.Hy.58, there is perhaps some slight indication of a much reduced third incisor 11.5 mm. distant from P_1 . There is no sign of this tooth in any other material referred to *Megalohyrax championi*.

The third molar is an elongate, relatively narrow, three-lobed tooth. The

anterior lobe is the broadest, the posterior the narrowest. Externally the lobes are divided by deep, anteriorly-inclined valleys, which run diagonally up to the main internal cusps. The anterior lobe is formed by the low, stoutly rounded protoconid, which wears into a longitudinal crescent, internally concave. The second lobe is formed by the similar, but slightly higher, hypoconid. The third lobe, which is considerably smaller and lower than the two preceding ones, is formed by the stout hypoconulid. This gives rise in wear to a similar crescentic pattern. On the lingual side of the tooth, the anterior cusp or paraconid is reduced to little more than a tubercle at the anterior horn of the first crescent. The strong, slightly compressed metaconid is the highest cusp of the crown; it receives the posterior horn of the first, and anterior horn of the second crescent. Its posterior edge usually shows a slight convexity in the position of the metastylid seen in *Titanohyrax*. In one or two specimens, for example C.M.Hy.6 (Pl. 4, fig. 1), a metastylid is quite well developed, and in C.M.Hy.59 (Pl. 4, fig. 2) the metastylid is comparable to that of *Titanohyrax*. Immediately behind the metaconid lies the entoconid, similar in form but of reduced height, and receiving the posterior and anterior horns of the second and third crescents respectively. The cingulum is developed externally in the valley between the lobes, and across the anterior face of the tooth, to a varying degree.

The second molar is shorter and broader than M_3 . It possesses only two lobes, separated by a deep, anteriorly inclined external valley. The anterior lobe is usually a little wider than the posterior. Otherwise the tooth is exactly like M_3 , with the third lobe replaced by a posterior development of the cingulum. Among the material from Rusinga there is an isolated second molar (520 '47, Pl. 5, fig. 2), which differs from all other second molars of *Megalohyrax championi* in the collection by reason of the relatively enormous accessory stylid, placed in the mouth of the external median valley. The stylid is associated with a poor development of the external cingulum; otherwise the tooth is perfectly normal. Examination of 50 lower molars of *M. championi* and over 100 lower molars of Oligocene and Pliocene hyracoids showed two things; first, that the size of this accessory stylid is unique in Tertiary hyracoid material; and second, that when an external accessory stylid is present in other specimens of *M. championi*, it is associated with an abnormally strong external cingulum. A similar but very much weaker stylid is sometimes present in *Procavia*. In a sample of over 60 Recent skulls it was found that the strongest development could be correlated with the possession of relatively high-crowned teeth. Simpson (1944: 43-44), has described a similar occurrence of an extra cusp in *Phenacodus*, as a possible expression of unit mutation.

Except for their smaller size and narrower anterior lobe, the first lower molar and third and fourth premolars are similar in all respects to M_2 . In the first and second premolar, paraconid, metaconid, entoconid, protoconid and hypoconid can all be recognised. In P_1 , however, the general relief, and the separation of anterior and posterior lobes are usually less clearly defined than in more posterior teeth.

The first lower incisor in both the male and female of *Megalohyrax championi* is a large, procumbent tooth, possessing a broad, flat, and pectinate terminal portion. The crown is deeply trifold, and the plane of wear, when present, truncates the pectination in a direction at right angles to the long axis of the tooth. The root is compressed almost at right angles to the crown, indicating that in life the latter lay in

a near horizontal plane, tilted very gently inwards. Of the three terminal pectinations, the dorso-external is the broadest, the median the narrowest. Frequently a small accessory tubercle is developed on the dorso-external edge of the crown, near the base of the pectination. Both surfaces of the crown are covered by enamel to a point about 3 mm. distant from the alveolar margin. The lower boundary of the enamel is entire, and runs straight across the tooth. The enamel sometimes shows faint annular wrinkling on the convex labial surface of the crown.

The second incisor of the female is very similar to the first. It lies somewhat external to I_1 , is less procumbent, and has the crown tilted more steeply inwards. This is reflected in the root, which is compressed in almost the same plane as the crown, and in the oblique wear surface truncating the extremity.

The second incisor of the male differs greatly. In its mature, worn condition it is a recurved, tusk-like tooth, larger than both the first incisor of the male and the second incisor of the female. The tooth is peg-like and of ovoid section, with the crown and root compressed in almost the same plane. The occlusal surface truncates the crown, but is slightly oblique to the long axis of the tooth. Enamel occurs on both faces of the crown, but the lower or proximal boundary of the enamel runs forward in the centre of the labial and lingual surfaces, and tapers back towards the

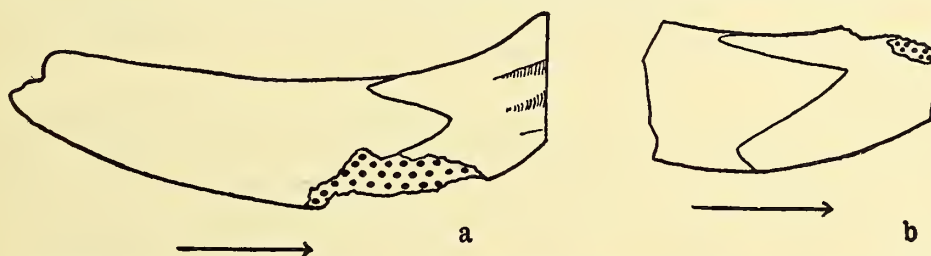


FIG. 7. The tusk-like second lower incisor found in the male of *Megalohyrax championi*. (a) C.M.Hy.8, (b) C.M.Hy.4I, both of the right side. Both $\times 2$.

root at the margins of these (Text-fig. 7). No terminal trifurcation normally remains, although there is a faint longitudinal grooving of the labial surface, similar to that seen in a well-worn second lower incisor of *Procavia*. In *Procavia* the enamel pattern of both first and second lower incisors corresponds exactly to the male second incisor in *Megalohyrax championi*. In young adults of *Procavia*, however, both teeth are terminally pectinate, and at this stage the lower border of the enamel is largely hidden within the alveoli. Moreover the first incisor of *Procavia* is procumbent, and during life suffers only minor truncation of the terminal lobes of the crown, by wear against the first upper incisor. The second incisor is inclined outwards, and appears to undergo some compensatory growth during life. In the male *Procavia* wear against the upper incisor, and compensatory growth, appear to be stronger than in the female. In consequence of this greater growth and the curved profile of the tooth, the second lower incisor of the male becomes progressively more tusk-like with increasing age. Eventually it is truncated by the increasingly oblique plane of wear, below the base of the terminal pectination. During this growth, the lower boundary of the enamel becomes visible, and in mature males there results a tusk-like second incisor, differing only in size from the corresponding tooth in *Megalohyrax championi*. In mature females of *Procavia*, wear on the second incisor is usually less

severe, and some remnant of the original pectination is preserved. A condition paralleling the male tusk seems to be found only in very old females.

This sexual dimorphism of the second lower incisor of *Megalohyrax championi* has an important bearing on Matsumoto's separation of the family Titanohyracidae. The main dental character by which this group is distinguished is the absence of a tusk-like second lower incisor, such as is said to characterise the Geniohyidae; although in the whole literature of Tertiary hyracoids only one tusk-like second lower incisor is clearly illustrated. This is figured by Matsumoto (1926, fig. 15c) as a second incisor of *Bunohyrax fajumensis*. It is indistinguishable from the second incisor of the male *Megalohyrax championi*. Schlosser's illustration of the second lower incisor in "*Mixohyrax*" *niloticus* (1911, pl. 12, fig. 3a) is misleading, since there is no means by which a tooth in that posture might be worn in the manner shown, unless the tooth were damaged. On the other hand, the only figure of a pectinate second lower incisor of *Titanohyrax* is that in Schlosser (1911, pl. 12, fig. 1). This tooth is only partially erupted, and completely unworn. Finally, Matsumoto himself (1926, fig. 8) figured a mandible of *Geniohyus mirus*, which appears to have a pectinate second incisor, differing in no essential from the semi-procumbent incisor found in the female of *Megalohyrax championi*. It seems likely that this supposed difference between Geniohyidae and Titanohyracidae is no more than a sexual variation, and that the specimen of *Titanohyrax* described by Schlosser probably represents an immature female.

The lower canine is a small tooth, very similar to that of the Oligocene species of *Megalohyrax*. It possesses a flat, slightly expanded, leaf-like blade, with faintly crenulate distal margin. The root is curved, and compressed in the same plane as the crown. The total length, including the root, is about 16 mm., and the maximum breadth of the crown about 5 mm. The enamel is smooth, and confined to the labial surface of the crown. It is uncertain whether a third lower incisor persists, even sporadically, in *Megalohyrax championi*. A single isolated tooth (817 '47c) may possibly be a third incisor. This tooth is very small, but otherwise similar to the first lower incisor of *M. championi*. The root is, however, compressed in the same plane as the trilobate crown. The tooth measures 13.0 mm. in length, and about 5.5 mm. across the crown.

The milk molars are well represented in a right mandibular ramus with dM_1 to M_1 (C.M.Hy.34, Pl. 3, fig. 1) and in the juvenile mandibles C.M.Hy. 62, 105 and 107 (Pl. 3, fig. 4). They are almost indistinguishable in crown pattern from the corresponding premolars, although in the unworn condition the cusps are sharper and more needle-like. The milk molars are perhaps a trifle larger than the premolars, but this may be due to the absence of crowding by the posterior cheek teeth. All possess four roots, except dM_1 , which has one anterior and two posterior roots. As in the upper dentition, M_2 seems to be fully erupted before the deciduous teeth are lost.

Post-cranial Skeleton

The specimen 334 '47 includes a complete left tarsus, together with portions of a right tarsus, associated limb-bones, metatarsals and phalanges. At its distal extremity the fibula is fused with the tibia, which has a strong internal malleolus. The astragalus and calcaneum are of hyracoid pattern, and closely resemble the

TABLE 4
MEGALOHYRAX CHAMPIONI

Upper Milk Dentition

	dM ²		dM ³		dM ⁴		M ¹		M ²	
	a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.
C.M.Hy.7 . .	10.4	10.3	12.1	11.2	13.2	14.0	17.4	17.6	18.3	19.5

Lower Milk Dentition

	dM ₁		dM ₂		dM ₃		dM ₄		M ₁	
	a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.
C.M.Hy.34 . .	10.0	6.0	11.4	8.0	13.2	8.8	15.2	10.2	17.5	11.7
C.M.Hy.62 . .			11.0	7.5						
C.M.Hy.63 . .					12.2	7.8	14.3	9.6	16.8	11.8
C.M.Hy.101 . .					13.6	8.8				
C.M.Hy.107 . .			11.3	7.5	13.7	8.1				

corresponding bones of Oligocene Geniohyidae figured by Schlosser (1911, pl. 13, figs. 1, 2). The fossa in the astragalus, which receives the internal malleolus of the tibia, is however deeper and more restrictive than in either Recent or Oligocene hyracoids, and is closed behind by a strong, postero-internal astragalular protuberance. The astragalus (Text-fig. 8*a, f, g*) lies almost directly above the anterior extremity of the calcaneum, and its head articulates with the navicular alone. The calcaneum (Text-fig. 8*a, e*) bears a small antero-external facet with which the flattened cuboid articulates. Externally the astragalus bears a strongly developed facet for the malleolus of the fibula. The disc-like navicular (Text-fig. 8*a, b, c*) is of reniform section, and occupies the entire anterior facet of the astragalus. Similarly, the external cuneiform (Text-fig. 8*a, d*), a bone of T-shaped section, occupies almost the whole anterior articular surface of the navicular; but a very small portion of the facet accommodates a small bone of boomerang shape, which may represent either the second cuneiform alone (Text-fig. 8*h, j, k*), or the fused first and second cuneiform bones. The cuboid (Text-fig. 8*a, l, m*) is a small and laterally compressed, rectangular plate of bone. Both the cuboid and internal cuneiform fit somewhat beneath the central axis of the tarsus, which is formed of the navicular and external cuneiform.

These characters indicate an extremely narrow tarsus and foot, with the central axis considerably developed at the expense of the lateral units. The deep socket to receive the internal malleolus of the tibia suggests a joint rigidly restricted, and adapted to movement in a single fore and aft plane. This view is confirmed by the associated bones, which include portions of a large metatarsal, and a number of diminutive metatarsals showing lateral compression. The latter are adult, and seem to represent reduced lateral digits. Completely ossified terminal phalanges of widely differing size also occur in this material. It seems probable that in the pes

of *Megalohyrax championi* only three, or at most four, digits were present, of which the third was extremely well developed (Text-fig. 17b). Schlosser (1911) refers to a similar, but apparently less pronounced, mesaxonic development in the Oligocene Geniohyidae of the Fayum.

If the astragalus and calcaneum are compared with those of ungulates, it is clear that in general shape and relative position they conform to the perissodactyl rather

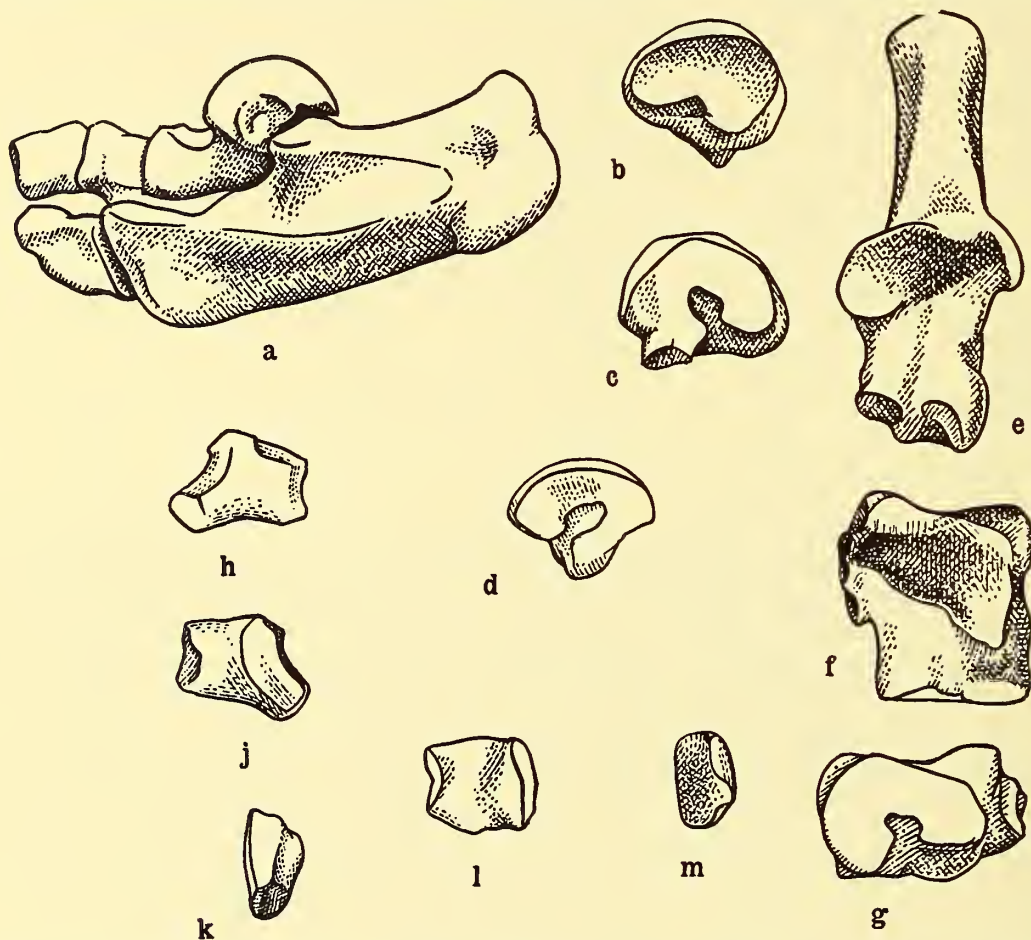


FIG. 8. The left tarsus of *Megalohyrax championi* (334 '47). (a) Lateral view of the articulated tarsus, showing the dorsal position of the navicular and external cuneiform in relation to the cuboid, (b) proximal surface of the navicular, (c) distal surface of same, (d) proximal surface of the external cuneiform, (e) dorsal aspect of the calcaneum, (f) ventral aspect of the astragalus, (g) distal surface of the astragalus, (h) medial aspect of the internal cuneiform, (j) lateral aspect of same, (k) posterior aspect of same, (l) lateral aspect of the cuboid, (m) posterior aspect of same. All natural size.

than to the artiodactyl pattern, and show the closest similarity to the hippomorph arrangement. The facets by which the astragalus and calcaneum articulate are of characteristic perissodactyl type; the manner in which they differ from those of *Equus* can be related to a digitigrade stance. Thus the internal and external facets are shifted slightly to the rear, to lend support to the shelf-like surface which receives the fibula, and become confluent across the postero-ventral margin of the astragalus, directly below the line of the tibia. A further difference lies in the

groove of the trochlea, which is wider and shallower than in *Equus*. It is, however, in the head of the astragalus, and in the proximal and distal surfaces of the navicular that the most astounding resemblances are found. In the other features *M. championi* merely shows a similarity to the horse exceeding that found in true perissodactyls; in this latter group of characters, the two patterns are almost indistinguishable.

The bones of the fore limbs of *M. championi*, apart from their greater size, correspond closely to those of *Procavia*. Notable differences are the absence of a supra-trochlear foramen in the humerus, and the fusion of the radius and ulna. This latter condition, very occasionally found in aged individuals of *Procavia*, again suggests a cursorial habit. The pattern of the carpus is unknown, but Schlosser (1911) recorded a pronounced serial arrangement in Oligocene Geniohyidae. There seems little doubt that the giant *M. championi* was fitted for rapid locomotion in open country. The most suitable habitat would be wooded savannah or parkland.

Numerous hyracoid limb bones, scapulae, ribs, vertebrae (including atlas and axis), and phalanges from Rusinga Island may be referred to *M. championi*. They all closely resemble the corresponding bones both in *Procavia*, and in the Oligocene Geniohyidae.

TABLE 5

MEGALOHYRAX CHAMPIONI

Dimensions of foot bones numbered 334 '47

	Max. length parallel to median line of foot		Breadth at posterior facet, transverse to median line of foot		Horizontal diameter of astragalar head		Breadth transverse to median line of foot	
Astragalus . . .	25	25	25.5	25.5	20	20		
Calcaneum . . .	55.5	56	23	23				
Navicular . . .	9						21	
Ext. cuneiform . . .	9						17.5	
Int. cuneiform . . .	17.2						7	
Cuboid . . .	15						7.2	

NOMENCLATURE AND SYSTEMATICS

The material was found at a number of different sites, but under conditions that indicated a fairly strict contemporaneity between them all. Any differences in the material appear, on analysis, to represent a continuous range of variation. There can be little doubt also, that, on a purely morphological basis, the entire assemblage can be referred to Arambourg's *Pliohyrax championi*, despite the poor preservation and inadequate nature of the holotype material. Dr. Leakey's recent discovery at Losodok of an immature palate and upper dentition, which is clearly conspecific with the Rusinga material, confirms this opinion. In the Losodok palate the third molar is not yet fully erupted, and at this stage the choanae lie between the unerupted posterior molars.

This Miocene species from East Africa differs greatly from the Pontian *P. graecus* of Samos and Greece. Both are large, with smooth skull roof, a general similarity of the lower cheek teeth, and a backward prolongation of the hard palate behind the upper molars; but these factors are insignificant when set against the following differences. *P. graecus* has a short, broad skull, with strongly arched zygomata, and small, closed orbit, placed high on the side of the skull. The upper molars extend behind the anterior limit of the zygomata, and the upper dentition is closed from second incisor to third molar. The lower dental series is closed from the first incisor to the third molar, and, in contrast to the East African material, the lower cheek teeth are high crowned and laterally compressed. In addition there is a strong third lobe in the third upper molar, and in the second and third lower molars of *P. graecus*.

The Rusinga material possesses a number of major characters, which, in combination, are shared by only one known family of hyracoids. These features, comprising the narrow, elongate, comparatively low skull, and the large fenestra on the inner surface of the shallow mandibular ramus, are only found associated in Matsumoto's *Geniohyidae*. Although rough-skulled, these are large, long-snouted forms, possessing very similar cheek teeth arranged in the same closed series, P_1 to M_3 below, and C to M^3 above. In these Oligocene forms, however, the anterior cheek teeth are not so profoundly molarised. *Bunohyrax* has no internal mandibular fenestra, but *Geniohyus* and *Megalohyrax* invariably possess some form of vacuity on the inner face of the mandibular ramus. In *Geniohyus*, however, this internal vacuity is probably a fossa, that is a depression, rather than a perforation of the inner wall of the ramus; and the lower border of the mandibular ramus is strongly deepened behind, in a manner quite foreign to the Rusinga material. The fenestration of the ramus of *Megalohyrax* corresponds almost exactly in size, position and form to that found in the Rusinga material, and the mandible deepens gradually and uniformly towards the rear.

Even in *Megalohyrax*, as defined by Andrews, Schlosser and Matsumoto, certain differences can be determined. In 1921 Matsumoto established identity between *Megalohyrax* Andrews and *Mixohyrax* Schlosser, and assigned the specimens described as *Megalohyrax* by Schlosser to a new genus, *Titanohyrax*. *Titanohyrax* is incompletely known, but despite Matsumoto's contrary opinion, there is reason to suppose that the genus comprises fairly long-snouted forms. Certainly there is no direct evidence that the snout was short, whereas there is some positive evidence that it was fairly long. If the characters quoted and illustrated by Andrews, Schlosser and Matsumoto for *Megalohyrax* Andrews and *Titanohyrax* Matsumoto are compared with those of the Rusinga material, then the last-named seems to lie midway between the two genera.

<i>Megalohyrax</i>	Rusinga material	<i>Titanohyrax</i>
Rough skulled.	Smooth skulled.	Smooth skulled.
I_2 tusk-like.	I_2 procumbent, pectinate, or tusk-like.	I_2 procumbent, pectinate.
Cheek teeth somewhat bunoid.	Cheek teeth less bunoid.	Cheek teeth still less bunoid.

<i>Megalohyrax</i>	Rusinga material	<i>Titanohyrax</i>
Enamel rumpled.	Enamel almost smooth.	Enamel almost smooth.
Upper cheek teeth brachyodont.	Upper cheek teeth slightly higher crowned.	Upper cheek teeth still higher crowned.
Upper molars almost quadrangular.	Upper molars trapezoidal.	Upper molars trapezoidal.
P ³ or P ⁴ to M ³ molariform.	P ¹ to M ³ molariform.	P ¹ to M ³ molariform.
Poor mesostyle.	Strong mesostyle in P ¹ or P ² to M ³ .	Strong mesostyle in P ² to M ³ .
Ectoloph not strongly W-shaped.	Ectoloph clearly W-shaped.	Ectoloph clearly W-shaped.
P ₃ or P ₄ to M ₃ molariform.	P ₂ to M ₃ molariform.	?P ₂ to M ₃ molariform.
No metastylid.	Poor to medium metastylid.	Fairly strong metastylid.
Lower C may be close to P ₁ or separated by short diastema.	Lower C when present close to P ₁ .	Lower C very close to P ₁ .

Closer examination shows that the differences outlined above are of limited significance. In the characters of the cheek teeth the differences exhibited by the Rusinga material, and for that matter by *Titanohyrax*, can be reconciled to *Megalohyrax* in terms of increased molarification, progressive along the lines of selenolophodonty and greater crown height. Thus the cheek dentition of the Miocene form may be derived from that of Oligocene *Megalohyraxes*, without radical change. It has also been shown that the apparent differences between the second incisors are an expression of sexual dimorphism, and that a tusk-like second incisor is not to be taken as a diagnostic generic character. The nature of the enamel also—a feature of great importance in Schlosser's classification of Oligocene hyracoids—is of little worth. Within a single hyracoid genus, or even within a species, there is considerable variation in the relative smoothness of the enamel. There seems little doubt that the Rusinga material only differs from the lower Oligocene species of *Megalohyrax* in small details. It is therefore referred to that genus, under the specific name *M. championi* (Arambourg). There is also some indication that *Titanohyrax* may be regarded as a precocious offshoot of the geniohyid stock. The generic name *Titanohyrax* is retained because there seems to be more than one species, but the separate family Titanohyracidae is probably not necessary.

Megalohyrax sp. (cf. *M. pygmaeus* Matsumoto, 1926)

(Pl. 7, fig. 2)

HORIZON AND LOCALITY.—Lower Miocene of Rusinga Island (Sites R.1, R.3 and R.107) and Karungu, Kenya Colony.

DESCRIPTION OF SPECIMENS.—(a) *C.M.Hy.60*.—Small fragment of a right mandibular ramus, bearing a single molariform cheek tooth, from Site R.107. It differs

from *Megalohyrax championi* only by being smaller. Posteriorly there is a depressed fracture of the thin infero-lingual wall of the ramus, corresponding to similar fractures commonly seen in front of the internal mandibular fenestra of other specimens of *Megalohyrax*. The solitary tooth is preceded by the alveoli of two other four-rooted teeth; it is either the fourth premolar or the first molar. Apart from its size, the tooth differs in no detail from the teeth of *M. championi*. The enamel shows the same annular striae. The dimensions are:

Depth of ramus at rear of tooth	.	19.0 mm.
Length of tooth	12.2
Breadth of tooth	7.9

(b) 522 '48.—Fragment of a left mandibular ramus, with the rear half of a posterior premolar (?), and the roots of the preceding tooth. Collected at Site R.3. The dimensions are:

Depth of ramus at rear of tooth.	.	17.5 mm.
Breadth of tooth	7.8

In view of the resemblance between the permanent and deciduous cheek teeth of *M. championi*, it is difficult to determine whether these two mandibular fragments represent a new species or not. In C.M.Hy.60 the solitary remaining tooth is preceded by the alveoli of two four-rooted teeth. Almost invariably the first premolar and first milk molar of *M. championi* possess three roots, two behind and one in front. Even in the rare examples possessing four, bifurcation of the anterior root invariably takes place well below the level of the alveolar margin. In C.M.Hy.60 the most anterior tooth represented had two separate and clearly divided anterior roots. It is obvious, therefore, that if C.M.Hy.60 appertains to *M. championi*, then the remaining tooth is in all probability P_4 or dM_4 , or an even later tooth. Moreover, the clear imprint of two roots on the hinder face of this specimen shows that the tooth immediately behind, in this event M_1 , was also fully erupted. Among the material referred to *M. championi* is a right mandibular ramus (C.M.Hy.34), bearing dM_1 to dM_4 and a newly erupted first molar. The amount of wear on the tooth of C.M.Hy.60 is considerably less than it is on the deciduous molars of C.M.Hy.34. Therefore, by reference to the fall of the deciduous teeth in *M. championi*, there is some indication that this tooth may in fact be P_4 in wear, in which case M_2 was probably also erupted. Thus, if C.M.Hy.60 is referred to *M. championi*, it would seem to represent an individual at least as mature as C.M.Hy.34 (which is known to belong to that species), and yet little more than half its size.

A radiograph of C.M.Hy.60 fails to show any sign of an unerupted permanent dentition, such as can be seen in a radiograph of C.M.Hy.34. Final confirmation that they are adult is supplied by sections cut through C.M.Hy.60 and 522 '48. These sections show no trace of the thick enamel, which caps the permanent cheek teeth in *Megalohyrax* at this stage of individual growth. In C.M.Hy.34 a similar section through the jaw ramus clearly shows the enamel capping of the unerupted fourth premolar.

There can be little doubt, therefore, that the two mandibles (C.M.Hy.60 and 522 '48) are adult or nearly so, and that a separate specific grouping is necessary. No new

specific name is proposed for the present, since the available material is insufficient to justify such a step. The following material confirms, to some extent, the existence of a separate, small species of *Megalohyrax*.

(c) *C.M.Hy.25*.—Crown of a right upper incisor of a male hyracoid, collected at Site R.1. The tooth corresponds in all details to the first upper incisor of *Megalohyrax championi*, but is considerably smaller, and describes an arc of a lesser circle. The dimensions are :

Length of portion preserved	.	.	.	15.0 mm.
Maximum breadth of external face	.	.	.	5.0
„ „ internal-anterior face	.	.	.	4.8
„ „ posterior face	.	.	.	3.7

This tooth is unlikely to be a milk incisor of *M. championi*, since study of Recent hyracoids suggests that deciduous incisors, in either sex, parallel the less specialised form of the adult female incisor. The tooth might be referred to *Meroëhyrax bateae*, but in view of its close resemblance to the adult incisor of *Megalohyrax championi*, it is kept in the same genus.

An isolated tooth (uncatalogued), which only differs from the tusk-like second lower incisor of the male *Megalohyrax championi* in its appreciably smaller size, has also been collected from the lower Miocene near Kamasengere, Rusinga Island.

(d) *K.364 '50*.—Isolated left navicular from Karungu. This bone is exactly similar to the navicular of *Megalohyrax championi*, but is smaller. The dimensions are :

Breadth, transverse to median line of foot	13.5 mm.
Length, parallel „ „ „	6.1

Genus BUNOHRAX Schlosser, 1911, emend.

Giant, long-snouted hyracoids, with brachyodont, somewhat bunodont cheek teeth. Mandible shallow, increasing gradually in depth to the rear. Upper molars roughly square, with flattened ectoloph, and poorly developed, almost longitudinal inner crests. External styles very weak, mesostyle antero-posteriorly compressed. Para- and mesostyle external to ectoloph, and not fully incorporated in the crown. Lower molars bunoid, with transverse ridges not fully developed. Inner and outer cusps almost opposite.

Type species *B. fajumensis* (Andrews), 1904; designated as the type species by Matsumoto (1926).

Bunohyrax sp.

(Pl. 7, fig. 3)

HORIZON AND LOCALITY.—Lower Miocene of Songhor, Kenya Colony.

DESCRIPTION OF MATERIAL.—*Sgr. 311 '48*. Isolated upper molar of a species of *Bunohyrax*, collected at Songhor. The tooth, probably a left M², is four-rooted and almost square. The enamel is smooth, except for some vertical wrinkling near the cingulum. The four main cusps are all stout, bunoid pyramids, the outer being a

little higher than the inner. The external styles and ectoloph are typical of *Bunohyrax*, consequently the ectoloph, at its anterior end, turns sharply outwards at right angles into the parastyle. The mesostyle is compressed to form a sharp re-entrant angle at the middle of the ectoloph. The inner cusps wear into weak, arcuate figures, of which the anterior end is only slightly external to the posterior. The cingulum is well formed on the external face of the tooth, linking the main external styles; it also forms an internal accessory style below the hinder edge of the protocone. The dimensions are: Length, 17.6 mm.; Breadth, 16.4 mm.

Another isolated upper cheek tooth, 38 '50, from R.1, Rusinga, is probably an upper premolar of a species of *Bunohyrax*.

Family MYOHYRACIDAE Andrews, 1914

Genus MYOHYRAX Andrews, 1914, emend.

(= *Protypotheroides* Stromer, 1922)

Very small hyracoids with fairly long, narrow snout and shallow mandible, showing rodent-like modifications of teeth and jaws.

Type species *M. oswaldi* Andrews, 1914.

DISCUSSION.—The genus *Protypotheroides* was founded by Stromer (1922) on material differing from *Myohyrax oswaldi* only in the presence of two enamel islands at the occlusal surface of each lower cheek tooth, and in the greater size of the teeth. This seems insufficient grounds on which to separate *Protypotheroides*. Indeed Hopwood (1929) has described under the name *M. osborni* material from the same area of South-West Africa, which is virtually indistinguishable from Stromer's type species *P. beetzi*.

Myohyrax oswaldi Andrews, 1914, emend.

(Pl. 5, figs. 3, 4; Pl. 6; Text-figs. 9-15)

(= *Myohyrax doederleini* Stromer, 1926)

DIAGNOSIS.—A moderately long-snouted, pygmy hyracoid. Skull fairly low and somewhat narrow. Zygoma commences above M^1 and rises sharply towards the rear, so that the glenoid fossa lies high above the palate. False palate extends at least as far back as M^3 . Mandibular ramus comparatively shallow, deepening gradually behind, with high, slender, pillar-like articular process and elongate articular condyle. Posterior angle of ramus with prominent hook-like process. Symphysis long and shallow. Dental formula $\frac{3 \ 1 \ 4 \ 3}{3 \ 1 \ 4 \ 3}$. P_4 or M_3 largest tooth in either jaw. Cheek teeth high crowned, prismatic, rooted. Enamel sometimes shows irregular annular wrinkling. Curved transverse ridges of enamel developed in wear on occlusal surface, paralleling condition in microtine rodents. Upper series closed, except for very short diastema between P^1 and C. Upper cheek teeth lopho-selenodont, approximately quadrangular, sloping back from base to apex. C and P^1 peg like; P^2 submolariform; P^3 - 4 molariform; M^3 much reduced. Three large, pro-odont upper

incisors, somewhat flattened labio-lingually, and slightly reduced in size from front to rear. In I^{1-2} enamel confined to labial surface. I^1 of male probably not different from that of female. Lower series not so tightly closed as upper, but evenly spaced throughout. Forward sloping lower cheek teeth of two sub-circular pillars. Anterior pillar generally narrower than posterior pillar in premolars, subequal or wider in molars. P_{2-3} sub-molariform, P_1 simpler; P_4 molariform; M_3 much reduced. Anterior incisors large, flattened, procumbent; enamel confined to labial surface. I_1 chisel-shaped, and slightly larger than the spatulate I_2 . I_3 and C styliiform. Milk molars brachyodont; less specialised than permanent cheek teeth.

DISTRIBUTION.—Type locality, lower Miocene of Kachuku, near Karungu Bay, Lake Victoria, Kenya Colony. *M. oswaldi* is also found in lower Miocene beds in other parts of East Africa (notably Rusinga Island), and in South-West Africa.

HOLOTYPE.—Fragmentary left mandibular ramus with P_2 to M_1 , not P_3 to M_2 (M.10610 Brit. Mus. (N.H.) Geol. Dept.), from Kachuku.

The extensive new collections from East Africa greatly increase our knowledge of this species, which was previously known only by the holotype, and a few jaw fragments from the region of Lüderitz Bay, South-West Africa (Stromer, 1926). In addition to the material described here, the Coryndon Museum, Nairobi, possesses many less complete specimens, chiefly collected at Karungu Bay and Rusinga. Included are 14 maxillary and 73 mandibular fragments, together with 54 isolated cheek teeth.

THE SKULL OF MYOHYRAX OSWALDI

This description is based primarily on the following specimens:

C.M.Hy.44.—An almost complete adult skull. This skull only lacks the anterior extremity of the snout, but is flattened laterally, and the cranium and occiput are badly crushed. Despite this damage, the right dentary is almost intact, and the right side of the skull anterior and ventral to the orbit, is well-preserved. The arching of the zygoma, facial region and dental series, and the symmetrical relationship of the portions preserved on the right and left sides, suggest that little distortion has occurred. Thus it is probable that the indications of a fairly long, low and moderately narrow snout and face are true characteristics.

C.M.Hy.52.—Portion of right mandibular ramus with P_4 to M_3 .

C.M.Hy.53.—Portion of left mandibular ramus with P_2 to M_3 .

C.M.Hy.54.—Portion of left maxilla with zygoma attached; P^4 to M^3 present.

K.49 '50.—Portion of left maxilla with P^2 to M^2 . Stromer (1926, pl. 41, fig. 4a) figured a very similar series of P^2 to M^1 , but he regarded the teeth as P^3 to M^2 , and identified them as *M. doederleini*.

K.89 '50.—Portion of right mandibular ramus with P_{2-4} .

K.97 '50.—Portion of left mandibular ramus with M_{1-3} , the third molar completely unworn.

K.118 '50.—Portion of left mandibular ramus with dM_4 .

K.161 '50.—Isolated left I^2 .

K.195 '50.—Isolated right I^1 .

K.196 '50.—Isolated upper incisor of the right side, probably I^3 .

C.M.Hy.44, 52, 53 and 54 were collected at R.1A, Rusinga Island. K.49, 89, 97, 118, 161, 195 and 196 were found at Ngira, Karungu Bay, in association with over 100 other jaw fragments and isolated teeth of *M. oswaldi*.

General Description of the Skull

The snout and face are fairly long, low and narrow, the maxillae gently convex, and ridged by the unerupted portion of the large, hypsodont cheek teeth. The zygoma is relatively deep and flat, and unites with the facial region approximately in line with the rear of M¹. It rises steeply towards the glenoid fossa, which, with the orbit, is placed very high in the skull. In the mid-line, the hard palate extends at least as far back as the rear of M³. The dorsal surface of the nasal and frontal bones rises gently in a straight line, just above the orbit, to the parietal region.

The mandibular ramus is fairly stout, but shallow in front. Following a slight anterior concavity of its inferior margin, it deepens gradually to the rear, along a gently convex curve. At no stage does it become very deep. The inner surface of the ramus is almost flat, the outer slightly inflated (Pl. 6, fig. 3). The long and shallow symphysis extends ventrally as far back as P₁. The alveolar edge of the ramus is slightly concave from above. A very short distance behind M₃, the anterior edge of the ascending ramus rises steeply. Its anterior margin appears to be robustly thickened, but the coronoid process is small, and does not project above the zygoma. The articular process is a high, slender pillar, which rises above the level of the posterior portion of the zygoma, and is capped by an antero-posteriorly expanded condyle. From this remarkable articular process the posterior margin of the ramus passes down into an equally unusual hook-like angular process. Below the hook, the angle of the jaw is rounded and unexpanded.

TABLE 6
MYOHYRAX OSWALDI
Dimensions of Skull

	C.M.Hy.44	C.M.Hy.52	C.M.Hy.53	C.M.Hy.54
Length of skull	est. 44			
Ant. margin of orbit to ant. extremity .	„ 21			
Ht. of skull from M ³ to frontal surface .	about 13			
Ht. of skull and mandible through articular process	„ 28			
Length of zygoma	„ 10			about 12
Depth of zygoma	3.3			3.0
Length of mandibular ramus	est. 38			
Ht. of ascending ramus from articular to lower margin	18.0			
Depth of ramus behind P ₂	4.0		5.8	
„ „ „ P ₃	5.4		6.5	
„ „ „ P ₄	6.5	6.9	7.2	
„ „ „ M ₁	7.3	7.7	9.0	
„ „ „ M ₂	8.5	8.3	10.0	
Thickness of ramus below M ₁		3.3	3.3	

Upper Dentition

The unreduced upper dentition forms a closed, gently arched series from I^1 to M^3 , broken only by a very short diastema between C and P^1 . The grinding teeth slope backwards from the maxilla; they are convex labially and concave lingually (Pl. 6, fig. 2). The posterior premolars and the molars are high, prismatic teeth, each with four small, well-formed roots. The enamel usually shows a very faint annular wrinkling. P^4 and M^1 are the largest teeth in the series, and the posterior molars decrease rapidly in size towards the rear (Pl. 5, figs. 3, 4).

The upper incisors are pro-odont and large; they closely resemble those which Stromer (1926: 121) referred to *Myohyrax doederleini*. The first incisor (Text-fig. 9a) is very slightly recurved, with a laterally compressed root, open at the end for the passage of the nerve. The crown is spatulate, convex labially and concave

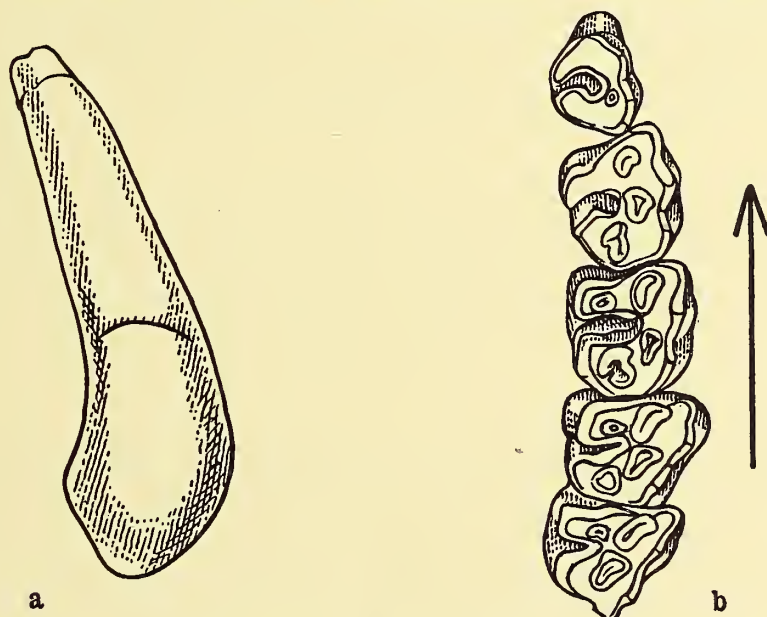


FIG. 9. *Myohyrax oswaldi*. (a) Antero-external aspect of a first upper incisor of the right side (K. 195 '50). $\times 8$. (b) Occlusal aspect of the upper second premolar to second molar of the right side (K. 49 '50). $\times 5$.

lingually. Enamel is restricted to a thick layer on the labial surface of the crown, and the occlusal surface wears to a chisel edge. Near the postero-external margin of the labial surface there is an ill-defined longitudinal groove, which is marked on the occlusal surface by a superficial infold of the enamel, corresponding in position to the notch mentioned by Stromer (1926).

The slightly smaller second incisor is very similar to the first, but its crown and root are compressed in almost the same plane, thus indicating the lateral position of this tooth in the premaxilla. This is emphasised by the obliquity of the concave occlusal surface. Enamel is present on the labial surface only. The third incisor is very little recurved; it possesses a laterally compressed and slightly open root. The crown is almost square in section, and enamel was probably present on each of its faces. The canine is a simple, stout, peg-like tooth with concave occlusal surface on the lingual side. The first premolar is similar, but slightly larger.

The first molar (Text-fig. 9b) may be taken as a standard example of the upper grinding teeth. The tooth is of trapezoidal section, being broader anteriorly than posteriorly, and its buccal surface is slightly oblique to the line of the maxilla. The enamel is thickest where it wears into transverse ridges. The worn occlusal surface comprises a hollowed-out centre of dentine containing four elevated islands of enamel-ringed cement. The two internal islands are usually smaller than the external pair. The occlusal surface is bounded by a raised rim of enamel, which is highest at the outer margin of the tooth. There is no indication of a cingulum, other than the peripheral styles described below.

Internally the tooth is divided by a deep, enamel-lined cleft into two antero-posteriorly compressed lobes, bearing the protocone and hypocone respectively. In wear these lobes form two transverse crests, the protoloph and metaloph, each containing one of the internal pair of cement islands. Each island lies immediately outside the corresponding main internal cusp. The anterior internal island is kidney-shaped, the other is a bilobed and posteriorly elongate island. At the external end of the transverse crests, weak proto- and metaconules may be developed to a varying degree.

The outer face of the tooth is strongly ridged by the external cones and styles, which extend to the base of the crown. Thus the outer ectoloph wall resembles a W, with the posterior V somewhat flattened. This is similar to the pattern of the ectoloph in early species of *Megalohyrax*. The inner margin of the ectoloph is indicated by the crescentic external cement islands, which lie slightly in front of the corresponding internal islands. The parastyle is often the lowest of the labial cusps. It is robust, and forms a strong anterior angle to the tooth. The mesostyle is the central and highest cusp of the entire crown. The much weaker paracone is probably marked by a step on the anterior slope of the mesostyle, and is delimited internally by the outer lip of the antero-external cement island. The mesostyle forms a marked vertical ridge on the outer surface of the tooth. Between this and the parastyle is a narrow groove, to which the paracone conforms. The metacone, the second highest cusp of the crown, lies almost directly behind the mesostyle, but forms a weaker ridge on the ectoloph than either the mesostyle or the parastyle. The inner flank of the metacone is formed by the outer lip of the postero-external cement island. The metastyle, a small cusp of approximately the same height as the parastyle, makes the posterior angle of the tooth. Despite its diminutive size, it forms a sharper ridge on the outer wall than the somewhat rounded metacone, but is less angular than the anterior styles. A faintly defined hypostyle may also be developed to a varying degree in the first molar. Andrews (1914: 170) stated that there is no mesostyle in *Myohyrax oswaldi*, and did not mention a metastyle, but his figures (pl. 28, figs. 6, 6a) show that the cusps to which I apply those names are present. The second molar is a reduced, but otherwise almost exact replica of the first molar. It is, however, less strongly inclined to the rear. The second molar to third premolar all possess four roots.

The third upper molar (Pl. 5, fig. 3a), is a tiny, splint-like, forwardly-directed tooth, considerably wider below than above. It is separated from M² at the base of the crown, but is in contact with it at the occlusal surface. The crown consists of a single pillar, and a very small posterior lobe, separated by a deep internal cleft, which

extends to the base of the crown. There is a less clearly marked external groove. The tooth is so completely reduced that it is impossible to distinguish the individual cusps with any certainty, and its functional value was small.

The fourth premolar differs from M^1 in its more perfectly rectangular outline, the anterior and posterior faces being approximately equal in breadth. Consequently the tooth is narrower than M^1 , and appears to be longer. The hypostyle is often more noticeable than in M^1 , whereas the metastyle is less strongly developed. The third premolar differs from the fourth only in its smaller size, the non-development of the antero-internal cement island, and in the approximately equal size of the metacone and mesostyle. The second premolar is a much smaller tooth than the third, and is relatively low-crowned. It possesses three well-formed roots, two behind and one in front. Externally the tooth is divided into a small anterior lobe and a larger posterior one by a shallow groove, which persists to the base of the crown. The individual cusps and styles are difficult to distinguish, but it seems probable that the mesostyle is not present. Internally the second premolar is divided into two lobes by a shallow valley, which makes hardly any feature on the inner face of the tooth. The antero-internal lobe or protocone is very weak, and bears no cement island. The postero-internal lobe or hypocone is larger, but the only island developed on the occlusal surface of this tooth is one of ovoid outline at the outer end of the median internal cleft; it corresponds to the postero-external island of more fully molarised teeth. Like the rest of the upper cheek teeth, the second premolar slopes towards the rear.

Lower Dentition

The unreduced lower dentition forms a closed, gently arched series from I_1 to M_3 . From the second premolar to third molar the teeth slope forwards. The fourth premolar is fully molarised, the second and third are sub-molariform (Pl. 6, figs. 1, 3). The third premolar to second molar are strongly hypsodont, with a considerable portion of the enamel-covered crown included within the mandible. Each of these four teeth possesses two roots, which are compressed from front to rear. The enamel shows fine annular wrinkles, which Stromer explained by reference to checks in the growth of the enamel.

The first and second lower incisors are only represented by their roots, preserved in the broken anterior extremities of C.M.Hy.44 (Text-fig. 10b) and C.M.Hy.53. From these two specimens it is clear that the anterior incisors were large and procumbent, with laterally compressed roots. It is most probable, however, that *Myohyrax oswaldi* and *M. doederleini* are synonymous (see p. 37), and well-preserved examples of lower incisors attributed to the latter species have been described by Stromer (1926) and Hopwood (1929). The latter wrote, "The incisors are procumbent; I_1 is chisel-shaped and I_2 subspatulate. Both are convex and covered with enamel on the labial surface, whereas their lingual surfaces are either flat (I_1) or gently concave (I_2) and entirely devoid of enamel . . . In *Myohyrax* the occlusal surface is on the lingual side of the tooth, is nearly parallel to the long axis, and is triangular in outline." The third incisor, canine and first premolar are preserved in C.M.Hy.44 (Text-fig. 10a). They are all very small, forward-inclined teeth, of simple styliform pattern.

The second premolar is a laterally compressed and relatively low-crowned tooth, with roots clearly divided at the alveolar margin of the mandible. There are two roots behind, and a single broad anterior root, which may divide within the mandible. The tooth is somewhat flattened on its inner surface, but is separated into two roughly equal lobes by a strong external groove. This groove does not extend to the base of the crown. The enamel is greatly reduced in thickness on the lingual surface of the crown. When the tooth is little worn, the anterior lobe is appreciably higher than the posterior, and the occlusal surface exhibits a pronounced inward slope (Pl. 6, fig. 3a). Andrews seems to have regarded this as the result of wear, but it is more likely to be an intrinsic feature of the unworn tooth. In well worn second and third premolars the occlusal surface is smooth and transversely convex, forming an exact counterpart to the concave occlusal surface of the opposing upper teeth. This wear

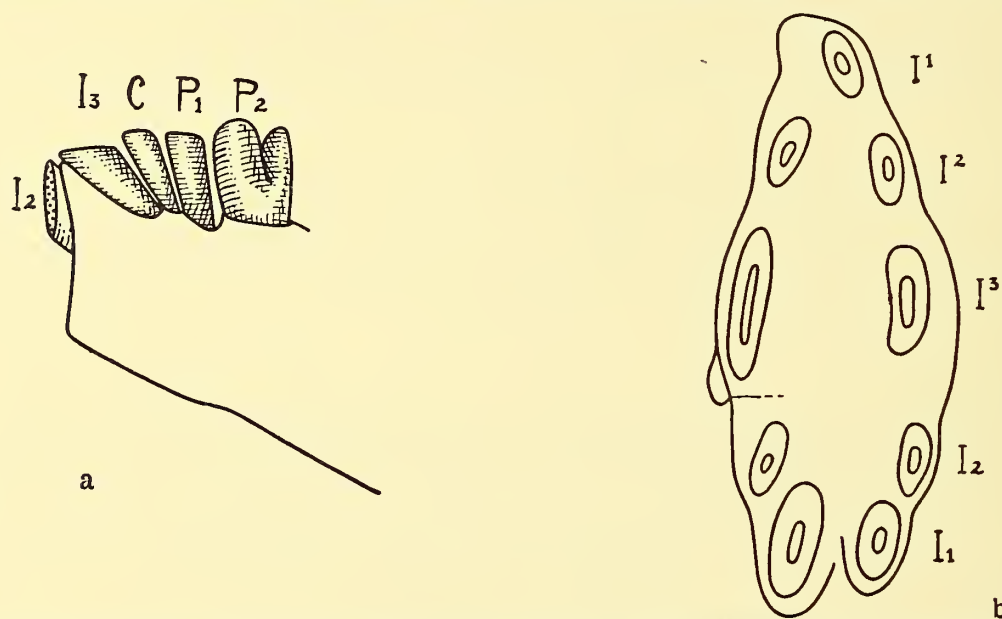


FIG. 10. (a) External view of the lower anterior dentition of the left side, and (b) a transverse section through the anterior region of the snout, as preserved in a skull of *Myohyrax oswaldi* (C.M.Hy.44). Both $\times 8$.

suggests that the main direction of mandibular movement was backwards and forwards.

Fundamentally the lower grinding teeth consist of two prismatic pillars of sub-circular section. These are separated by strong internal and external median grooves. The grooves almost completely constrict the tooth, and descend vertically to a point just above the lower limit of the enamel. The external groove always lies very slightly in front of the internal groove, and the anterior pillar is usually the longer. The occlusal surface consists of two hollowed-out areas of dentine, surrounded by a raised rim of enamel, which is often reduced or even suppressed at the anterior and posterior internal angles of the tooth. This enamel rim is higher at the inner margin of the tooth. The enamel is usually developed equally on the labial and lingual surfaces, but is thickest where it runs transversely across the crown. No cement

islands are developed at the occlusal surface. The highest point of the crown is formed by the postero-internal angle of the anterior pillar, which probably represents the metaconid of less specialised hyracoids. The antero-internal angle corresponds to the paraconid, and the external convexity of the anterior pillar is no doubt equivalent to the protoconid of less hypsodont forms. The posterior pillar is slightly lower than the anterior. Externally it carries a hypoconid, and on its inner margin an elevation possibly representing an entostylid. The paraconid is separated from the metaconid by a vertical groove, which extends down to the alveolar margin. An isolated lower cheek tooth from Karungu (British Museum M.10611) was referred to *M. oswaldi* by Andrews (1914: 170-71), and described by him as a posterior molar with a third lobe. It is probably a first molar or fourth premolar of the right side, in which the supposed third lobe represents the paraconid, isolated by an unusually strong antero-internal groove. In the extensive collections of lower cheek teeth now available from Karungu

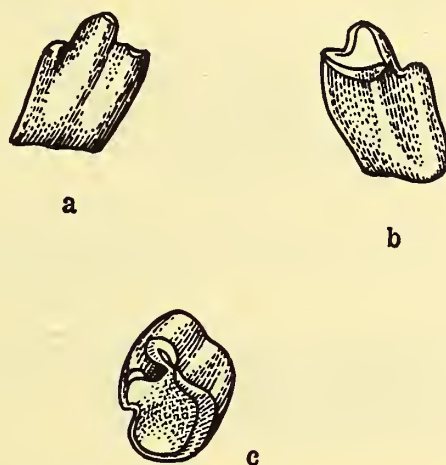


FIG. 11. (a) Lingual aspect, (b) labial aspect, (c) occlusal aspect of an unworn third lower molar of the left side in *Myohyrax oswaldi* (K.97 '50). Approx. $\times 10$.

and Rusinga, the development of this groove varies considerably. In a few examples it approximates to the condition in M.10611, in others it is barely perceptible. Most of the material exhibits an intermediate condition.

Individual members of the lower grinding dentition differ from this basic pattern in the following details. The third premolar is a relatively long tooth, laterally compressed and internally flattened. The median internal and external grooves do not quite reach the base of the erupted portion. The enamel is in general thicker on the labial surface. The fourth premolar is normally the highest member of the series, and conforms exactly to the general description given above. The anterior pillar is usually narrower than the posterior. In contrast to this the first and second molars tend to possess a broader anterior pillar. The third molar (Text-fig. 11) consists of a single prismatic column, corresponding exactly in pattern to the anterior pillar of the first molar, with the second pillar of that tooth represented only by a low, laterally-compressed heel or talonid. Externally the talonid is separated from the main body of the tooth by a shallow, vertical groove, running to the base of the crown. A similar groove separates the paraconid and metaconid. Internally the

talonid is defined by a deep cleft, which extends only a short distance from the occlusal surface.

At a very advanced stage of wear, the posterior grinding teeth take on a brachyodont appearance. This can be seen in K.94 '50 (Text-fig. 12) and K.147 '50,

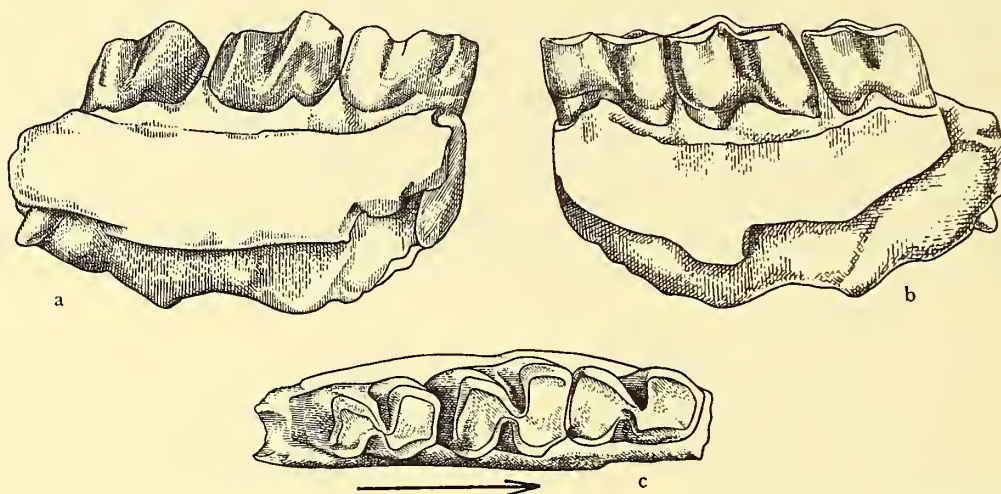


FIG. 12. The appearance of the cheek teeth in aged individuals of *Myohyrax oswaldi*. (a) Lingual aspect, (b) labial aspect, (c) occlusal aspect of a left mandibular fragment with fourth premolar to second molar (K.94 '50), showing the brachyodont appearance of the teeth through excessive wear. Approx. $\times 5$.

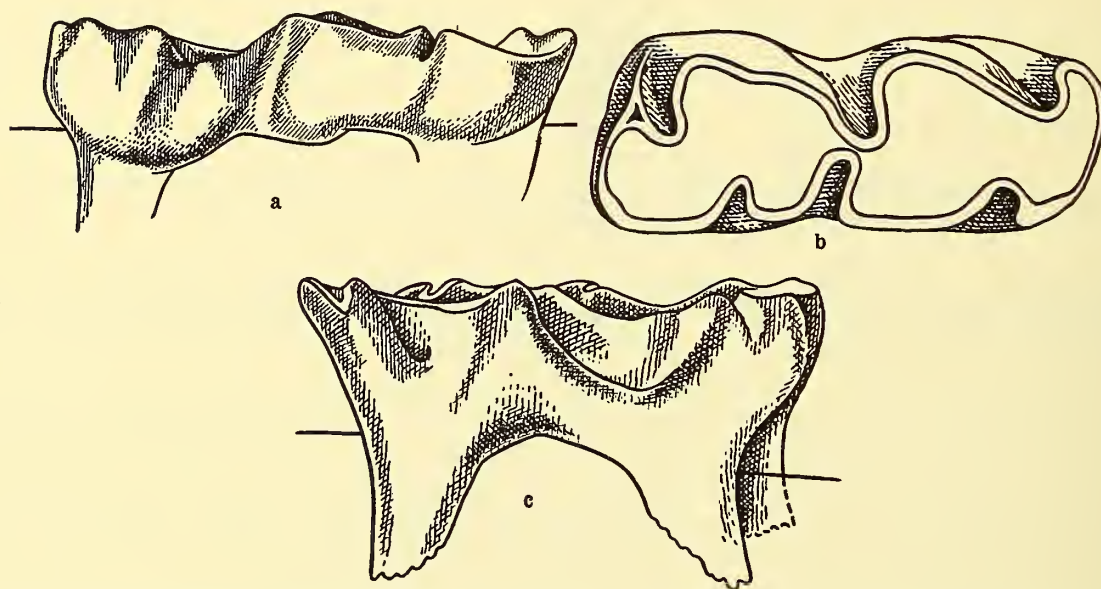


FIG. 13. The lower milk dentition of *Myohyrax oswaldi*. (a) Lingual aspect, (b) occlusal aspect, (c) labial aspect of a posterior milk molar of the left side (K.118 '50). $\times 15$.

mandibular fragments with P_4 to M_2 , and with M_1 , respectively. Here the roots are erupted above the alveolar margin, and the occlusal surface truncates the crown at a very low level. Wear has proceeded below the origin of the antero-internal groove, so that there is no clear separation of the paraconid and metaconid.

Milk Dentition

The lower milk dentition of *Myohyrax oswaldi* is represented by a portion of a left mandibular ramus, K.118 '50, bearing a solitary deciduous molar (Text-fig. 13). This specimen was collected at Ngira, near Karungu Bay. Its identity is proved by the characteristic prismatic third and fourth premolars, which lie unerupted in their crypts.

The milk tooth, which is a fourth milk molar, is extremely long and low-crowned, with four well-formed roots, dividing above the alveolar margin. The tooth possesses a high, somewhat compressed metaconid, and stout, bunoid proto- and hypoconid, separated by a forward-inclined and deeply incised external median valley. The paraconid is small, and cut off from the metaconid by an antero-internal infolding of the enamel. The entoconid also is small. Its growth is restricted by an enormous styler development, which forms an appreciable third lobe at the postero-internal

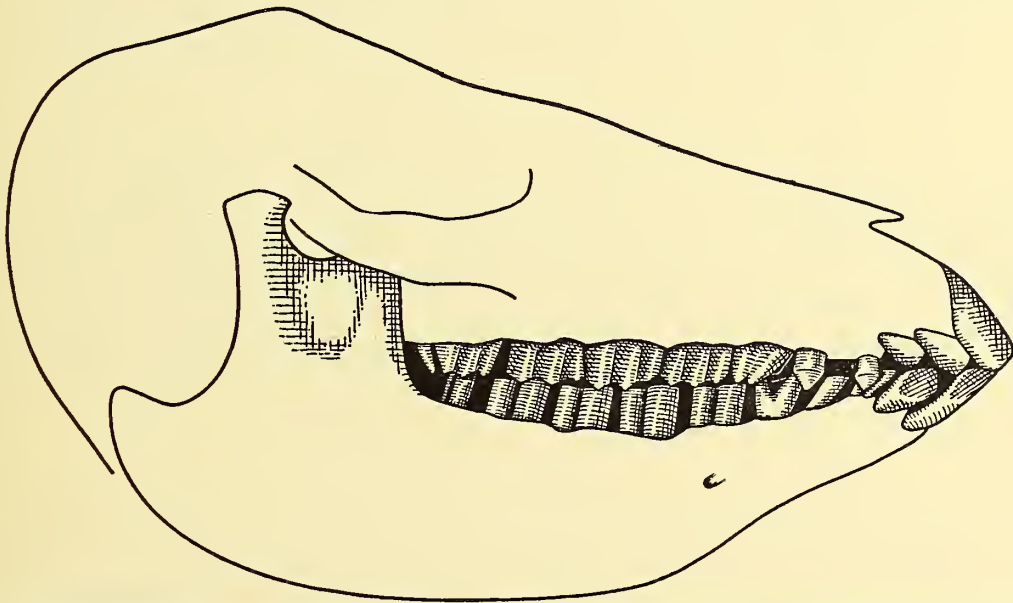


FIG. 14. Reconstruction of the skull of *Myohyrax oswaldi*, based on an almost complete skull (C.M.Hy.44).
× 3.

angle of the tooth, and makes the highest point of the crown. Similarly there is another large stylid at the antero-external angle of the tooth, confluent internally with the paraconid. This latter stylid is separated from the protoconid by a small valley. The posterior stylid is divided in like manner from both the hypoconid and entoconid. The maximum dimensions of the tooth are, length 4.6 mm., breadth 2.0 mm. Two posterior roots and a single anterior root of the third milk molar are also preserved, immediately in front of the tooth.

Without these stylids, the tooth differs little from the brachyodont molars of contemporaneous browsing hyracoids, and may indicate the lines along which specialisation of the adult *Myohyrax* molar has taken place. If this assumption is correct, then the principal elevations at the labial margin of the adult molar represent the protoconid and hypoconid, while those at the lingual margin represent the metaconid and entoconid, with the paraconid and entoconid greatly reduced.

Stromer (1926, pl. 41, fig. 5) figured and described a similarly brachyodont and four-rooted tooth as an upper milk molar of *Myohyrax doederleini*.

Reconstruction of the Skull

A reconstruction of the skull of *M. oswaldi* (Text-fig. 14) has been produced by adjusting Stromer's figures of the snout of *M. doederleini* (1926, pl. 41, figs. 2, 11) to the skull C.M.Hy.44. Stromer stated that the nasal bones in *M. doederleini* are elongate, and there is perhaps some suggestion of this in the damaged dorsal portion of the snout in C.M.Hy.44. Anteriorly extended and protruding nasals, comparable to those found in *Megalohyrax*, have therefore been added to the reconstructed skull.

The reconstruction emphasises the long snout. This is accompanied by an anterior extension of the zygoma in relation to the molars, which exceeds that found in *Sagatherium*, and even in *Pliohyrax*. A considerable length of snout is required nevertheless to accommodate the elongate cheek teeth, and, in particular, the unreduced upper incisors, a feature of *Myohyrax* that is unique among known hyracoids.

POST-CRANIAL SKELETON OF MYOHRAX OSWALDI

No portion of the post-cranial skeleton of *Myohyrax* has been found in East Africa to date, and the genus is represented solely by a very few isolated tarsal bones, vertebrae, and fragments of limb bones from South-West Africa, which Stromer (1926) referred to *M. doederleini*. They are roughly of equal size to the corresponding bones in a large brown rat. If the relative size of head and body was at all comparable to the condition found in *Procavia*, then the overall length of *M. oswaldi* was about 20 cm.

DISCUSSION

Stromer (1926) distinguished two contemporaneous and overlapping species of *Myohyrax* in the lower Miocene beds of South-West Africa, *M. oswaldi* Andrews, and *M. doederleini*. The two species cannot be separated by means of their dental characters, as shown in his figures. The only specific differences given by Stromer are :

- (1) A well developed antero-internal fold defining the paraconid in the cheek teeth of *M. oswaldi*, which is only indicated in *M. doederleini*.
- (2) The slightly greater size of the teeth in *M. oswaldi*.

At Karungu nearly 80 mandibular specimens of *M. oswaldi* were found in close association. The variation in their dental pattern is more profound than that employed by Stromer as a specific character ; and it is significant that among these 80 specimens the strongest development of the antero-internal fold is more frequently encountered at the lower end of the size range. Moreover, the variation in size in *M. oswaldi* and *M. doederleini*, when both groups of material are taken as a whole, falls within the compass of recorded ranges in Recent hyracoid species. Consequently it is better for palaeontological purposes to regard *M. doederleini* as a synonym of *M. oswaldi*.

Diet and Habit

The most exact parallel to the peculiar hook-like angular process, characteristic of the mandible of *M. oswaldi*, is found in rodents of the sub-family Microtinae, where this process chiefly serves for the attachment of the superficial portion of the m. masseter lateralis. Here this muscle is directed almost horizontally, and acts, in conjunction with the deep masseter lateralis and the anterior portion of the temporalis, to exert a powerful forward pull on the mandible. Thus the principal forces related to gnawing, and the forward-upward thrust employed in grinding the resistant food, are developed. In view of the strikingly similar coronoid and angular processes, and dental characters, it is not unreasonable to assume that the angular process in *Myohyrax* was developed in relation to a similar mechanism, and that the grinding of food was mainly effected by a longitudinal movement of the lower jaw. This is in complete accord with the convex lower, and concave upper surfaces of wear, particularly on the anterior cheek teeth. It is difficult to see how such wear could result from any appreciable lateral movement during grinding.

Ample proof of the resistant nature of the diet is afforded by the elongate battery of high-crowned cheek teeth, and the development of structures apparently related to differential movement of the jaws. This is substantiated by the extremely high position of the glenoid. A temporo-mandibular joint situated high on the skull is common in forms that live on a tough diet. It is presumably related to a posterior shift of the grinding centre of the dental battery, which increases the pressure applied at the occlusal surface, but must also involve an increase in gape, and an elongation of the masticatory muscles. In *Myohyrax* the development of a posterior grinding centre is not so extreme as in rodents, where a considerable diastema is formed, and the anterior teeth are suppressed. Nevertheless, the principal grinding teeth lie far back, close to the plane of the articulation. This backward shift of the grinding centre also explains the forward extension of the zygoma, relative to the teeth, mentioned previously (p. 37).

Two important dental characters confirm this suggestion of a longitudinal grinding action. The more striking is exhibited by the occlusal surface of the posterior cheek teeth. The molars of specialised microtine rodents possess an occlusal surface bearing transverse, curved and thickened ridges of enamel. The curves are opposed in the upper and lower jaw. Disruption of the resistant food is brought about by a relative displacement of the tightly engaged teeth in a fore and aft direction. The curved blades of enamel gliding past each other act as efficient shears. The posterior cheek teeth of *M. oswaldi* also develop their thickest enamel as curved, transverse ridges, opposed above and below, but parallelism is not exact. In Microtinae the lower, posteriorly-convex enamel ridges lie at the front of the lobes of each tooth, and the upper, anteriorly-convex ridges lie at the rear: in *Myohyrax* the positions are reversed (Text-fig. 15). Neither is the development of these transverse shearing blades so perfect. The strongest of these crests in *Myohyrax* are internal above and external below. C.M.Hy.44 shows that in life the posterior upper teeth lay slightly outside the lower teeth, bringing the principal upper and lower crests into opposition. The second important feature of the dentition in *Myohyrax* is the insertion of the grinding teeth. The forward slope of the lower, and backward slope of the upper

molars, also developed in microtine rodents, affords a stable grinding structure when the lower jaw closes in a predominantly forward movement.

The exclusion of enamel from the lingual surface of the anterior incisors is a condition common in rodents, but rare, probably unique, in Hryacoidea. The pro-odont upper incisors and the terminal restriction of the enamel suggest that the gnawing habit, if present, was unimportant. As Hopwood suggested (1929), it seems likely that the diet was mainly confined to seeds, extracted by the forcep-like incisors. The seeds could be hulled by rolling between these incisors, before the food was passed

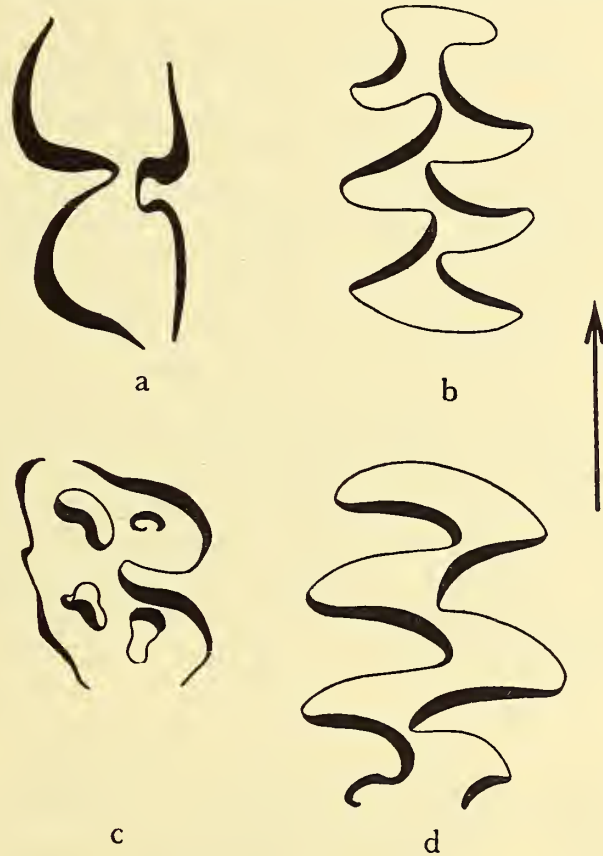


FIG. 15. The enamel trace developed at the occlusal surface of the molars in *Myohyrax oswaldi* and microtine rodents. (a) A lower left molar of *M. oswaldi*, (b) a lower left molar of a microtine rodent, (c) an upper right molar of *M. oswaldi*, (d) an upper right molar of a microtine rodent. (b) and (d) after Hinton. Not to scale.

back to be ground between the cheek teeth. The glenoid should prove to be shallow and extensive to accommodate the elongate articular condyle, and to permit a differential movement of the jaws. Although a pro-odont arrangement of the incisors in rodents may be associated with a burrowing habit, there is little reason to believe that *M. oswaldi* was fossorial. A fossorial life involves considerable strain and wear at the incisors, which in burrowing rodents tend to become greatly enlarged at their proximal end, and to grow persistently. The lower incisors frequently extend back within the mandible as far as the third molar or the articular condyle. No such exaggerated development is found in *Myohyrax*. Both Stromer and Hopwood have

suggested that the Namib fauna, including *Myohyrax*, lived under savannah or veldt conditions.

The simulation of many rodent characters in *M. oswaldi* was remarkably advanced. Only six upper incisors of *Myohyrax*, all modelled on the same pattern, are known. It seems improbable that *Myohyrax*, in all else so completely rodent-like, should have retained or developed a sexual dimorphism of the upper incisors that is common in less specialised hyracoids, but is unrepresented among rodents, and is totally unsuited to the mode of life suggested above.

AFFINITIES OF MYOHRACIDAE

Matsumoto (1926) suggested that the short-snouted Pliohyracidae of his classification show the closest relationships to the Myohyracidae. The reason for this seems to lie in his mistaken assumption of a shortened snout in *Myohyrax*, which otherwise differs from *Plio-hyrax* and *Saghattherium* to a most marked degree. In its dental characters, *Myohyrax* represents a strongly divergent stock, showing extreme specialisation of the cheek teeth (and mandible), but retaining an incisor development, which is probably somewhat primitive. The three families Geniohyidae, Pliohyracidae and Myohyracidae clearly belong to the same order, but the Myohyracidae are an aberrant and ancient offshoot of the hyracoid stem, and their relationship is more remote than Matsumoto seems to have implied. Even the common occurrence of a long snout in Geniohyidae and Myohyracidae is of limited significance, being associated in one group with lengthy anterior diastemata, in the other with a primitive lack of diastemata and an anomalous forward extension of the zygoma. A strictly graded scale of affinities might, however, place the Myohyracidae closer to a long-snouted family, than to one which already, in early Oligocene times, exhibits a characteristic shortening of the snout.

Family PROCAVIIDAE Thomas, 1892

Sub-family SAGHATHERIINAE subfam. nov.

Small to medium-sized hyracoids, with short snout, fairly deep jaw, usually unreduced dentition. Upper molars, where known, show fairly good development of both longitudinal and transverse crests. Posterior third lobe in M_3 .

Genus MEROËHYRAX gen. nov.

Medium-sized, short-skulled hyracoids. Mandibular ramus deep and externally convex, convexity not caused by the large, oval fossa on the inner surface of the mandible. Brachyodont, buno-selenodont lower cheek teeth, closed at least from C to M_3 . M_3 longest tooth of lower jaw, third lobe present. Posterior premolars molariform.

Meroëhyrax bateae sp. nov.

(Pl. 7, fig. 1; Text-fig. 16)

DIAGNOSIS.—As for genus.

DISTRIBUTION.—At present only known from the lower Miocene of Rusinga Island (Sites R.1 and R.3A), Kenya Colony.

HOLOTYPE.—Coryndon Museum 324 '47 from R.1, Rusinga. Portion of a right mandibular ramus with P_3 to M_3 , the alveoli of P_{1-2} , and part of the root of the canine. The fragment lacks the anterior extremity, most of the lower margin, the angle, and the ascending ramus.

DESCRIPTION.—The ramus is stout and deep, and the tooth-row conforms closely to the external convexity of the jaw (Pl. 7, fig. 1a, b, c). The most notable feature is the large, ovoid, internal fossa, lying immediately below the roots of the cheek teeth, and extending from the rear border of M_2 to the middle of P_2 (Pl. 7, fig. 1b). Its long axis is slightly lower anteriorly than posteriorly. The fossa is deep, but

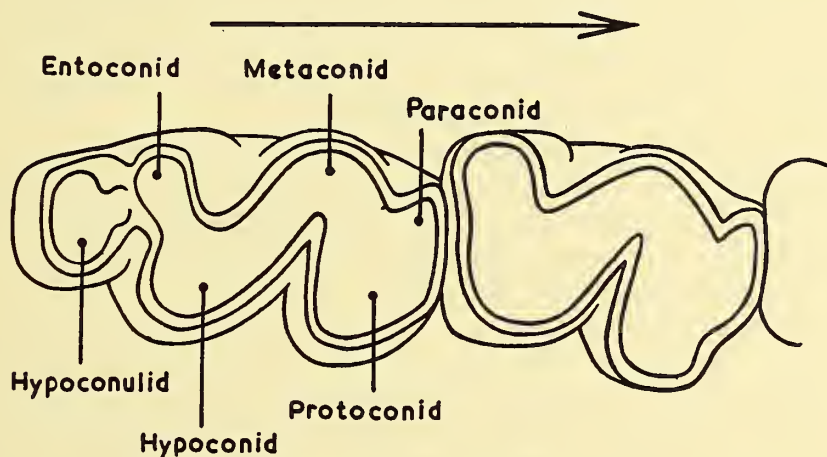


FIG. 16. Occlusal aspect of the second and third lower molars of the right side in *Meroëhyrax bateae*, showing the relative positions of the protoconid and metaconid. Drawing based on the holotype (324 '47). Approx. $\times 4$.

causes no corresponding elevation on the outer surface of the ramus. It is apparently a natural feature of the mandible.

The anterior edge of the base of the ascending ramus is strongly grooved. Commencing external to the talonid of the third molar, from which it is separated by a sharply defined shelf, the groove runs diagonally inwards and upwards. There is some indication that a canal passed through from the groove to the inner surface of the ramus. The canal, like that in *Procavia*, is just above the level of the cingulum in M_3 .

The moderately low-crowned, bunio-selenodont teeth form a closed series from C to M_3 . The third molar, which possesses a prominent posterior third lobe, is the longest tooth, and M_2 is the broadest tooth of the series. The teeth decrease in size forward. In marked contrast to the majority of Tertiary hyracoids, the anterior lobe

of each molar is slightly broader than the posterior. This depends principally on a posterior shift of the protoconid relative to the metaconid, so that the two cusps are more nearly opposite each other than is usual (Text-fig. 16). In the molariform third and fourth premolars, the posterior lobe is the broader, and the position of the protoconid is more normal.

All the cheek teeth appear to have four roots, except M_3 , which has five, and P_1 , which probably has three, or perhaps two roots. There is a possibility that the fragment of root believed to represent the canine may in fact be an unpaired anterior root of P_1 , but this is unlikely.

The cheek teeth, which are in an advanced condition of wear, conform closely to the arrangement usual in brachyodont hyracoids, but differ in absolute size and relative proportions. The narrow, elongate third molar possesses three external cusps, divided by very deep external valleys, which run forward to the main internal cusps, the metaconid and entoconid. The protoconid is stout and rounded, the hypoconid and hypoconulid are similar. The hypoconid is the stoutest and highest of the three outer cusps, all of which are crescentic in wear. The internal cusps comprise a much reduced but distinct paraconid, and moderately compressed metaconid and entoconid. Although the entoconid is strongly developed, the metaconid is the highest cusp of the crown. A metastylid is not present, and the cingulum is only prominent on the anterior face of the protoconid. An isolated lower M_3 , 499 '49 from R.3A, is also referred to this species.

The second molar is broader and shorter than the third; it has no third lobe. Otherwise, except for a somewhat stouter entoconid, its structure agrees with that of M_3 . The first molar, and third and fourth premolars are smaller replicas of M_2 . The alveoli of the first and second premolars are preserved in the upper edge of the ramus, but the roots are not clearly defined.

DISCUSSION.—Although *Geniohyus* is the only other hyracoid known to possess a comparable mandibular fossa, this new species differs from all Geniohyidae in its appreciably smaller size. In addition the deep and strongly arched mandible, and the externally convex dentition, tightly closed from C to M_3 , suggest the possession of a short snout. The molar teeth also show many differences of detail. Both *Prohyrax* and *Pliohyrax* appear to be short-snouted forms, but the former is a little smaller than *Meroëhyrax*, with higher crowned teeth, and *Pliohyrax* is very large, with fairly high, laterally-compressed lower cheek teeth, and a strongly developed third lobe in both the second and third lower molars. Comparable differences are found in *Titanohyrax*, and in the stout, bunoid lower molars referred to *Pachyhyrax*.

The genus *Sagatherium* comprises small to medium-sized, moderately short-skulled species, some of which, notably *S. antiquum* and *S. euryodon*, conform closely in size to the holotype of *Meroëhyrax bateae*, but occasionally there is a short diastema between the canine and first premolar. In many species of *Sagatherium* the jaw ramus is deep, and increases rapidly in depth towards the rear. For example a specimen of *S. antiquum* figured by Schlosser (1911, pl. 13, fig. 12) closely resembles the probable shape of this Rusinga mandible, and carries a lower tooth row of almost the same length. The more complete material described by Matsumoto (1926) shows a fairly straight lower tooth row, except in certain individuals of *S. euryodon* and *S. annectens*. In the former the teeth are extraordinarily similar in size and crown

TABLE 8
MEROËHYRAX BATEAE

Dimensions of Mandible

	Coryndon Museum 324 '47f
Length of mandibular fragment	76
Distance from ant. face of P ₃ to ant. extremity preserved	11
Depth of ramus at rear of P ₄	26
" " " " M ₁	28
Thickness of ramus below M ₂	10
Thickness of ramus in floor of fossa	2
Height of fossa	16
Ant.-post. diameter of fossa	30
Distance from upper margin of fossa to alveolar edge	5
Distance from lower margin of fossa to lower edge of ramus	4

Lower Dentition

		P ₁		P ₂		P ₃		P ₄		M ₁		M ₂		M ₃	
		a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.	a.p.	tr.
324 '47f	R1	c.5		c.6		6.5	4.8	8.0	5.8	10.0	7.1	10.5	7.5	15.0	7.2
499 '49	R3A													15.3	7.6

pattern to those of *M. bateae*; although *S. euryodon* appears to possess a comparatively shallow mandibular ramus. Schlosser's figure of *S. majus* (1911, pl. 10, fig. 7) shows a very slight backward inclination of the anterior external crescent, which gives rise to anterior and posterior lobes of subequal breadth. As a rule, however, the third lower molar is proportionately broader in *Saghattherium* than in *Meroëhyrax*.

By combining certain of the characters of *Saghattherium antiquum*, *S. annectens*, *S. euryodon* and *S. majus*, a composite mandible might be constructed almost identical with that of *Meroëhyrax*, except for the internal fossa. The fossa differentiates sharply between the two genera. In this one character *Meroëhyrax* approximates more closely to *Geniohyus*; but even this resemblance is limited. In *Geniohyus* the internal mandibular fossa is larger, almost rectangular in outline, and causes a considerable prominence on the outer surface of the ramus. An internal mandibular fossa is absent from all specimens of *Saghattherium*, and is present in all adequate material referred to *Geniohyus*; thus there is no evidence to suggest that such a fossa might be a sexual character in some hyracoids. At present it seems wiser to refer this mandible to a new genus, *Meroëhyrax*. The specific name commemorates the late Miss Dorothea M. A. Bate.

IV. HYRACOIDEA *incertae sedis*

The exact affinities of the following specimens cannot be determined at present :

1. Mb.188 '49 from Maboko Island and 758 '47 from R.1, Rusinga Island, Kenya Colony. Two adult astragali, slightly smaller than those of *Megalohyrax championi*, but of similar pattern. Also Mb.189 '49 and Mb.190 '49 from Maboko Island ; two upper male I¹, very similar to those of *M. championi*, but slender and less recurved.
2. Three isolated upper cheek teeth, 381 '48 and 548 '47 from R.106, Rusinga, and C.M.Hy.98, site unknown. Completely molarised teeth, only differing from the upper molars of *Megalohyrax championi* in the low mesostyle, the shelf-like anterior cingulum, and the well developed transverse crests, similar to those found in *Prohyrax tertiarius* Stromer. Possibly upper cheek teeth of *Meroëhyrax bateae*. The dimensions are :

	Length	Breadth
381 '48	15.0 mm.	13.2 mm.
548 '47	c. 15.0	c. 14.0
C.M.Hy.98	12.0	10.5

3. Isolated hyracoid incisor, 373 '47 from R.1A, Rusinga. Corresponds in pattern to anterior lower incisor of *Megalohyrax championi*, but of very small size. Length 13.7 mm., breadth of crown c. 2.8 mm. Occlusal surface at right angles to long axis of the tooth, and strong torsion between crown and root, suggest that the tooth is a procumbent first incisor of a small species, not a reduced lateral incisor of a large form.
4. 754 '50 from R.3 and 934 '50 from R.106, Rusinga, and K.42 '50 from Ngira, Karungu. Three isolated lower anterior incisors, similar to those of *Megalohyrax championi*, but with six terminal pectinations instead of three. Hahn (1934) has recorded a very occasional milk incisor of *Procavia* possessing more than the normal number of pectinations.

V. ORIGINS OF HYRACOIDEA

Ameghino believed that the hyracoids and notoungulates were intimately related. The view has been revived from time to time by various authors, who have suggested that Ameghino's family Acoelodidae may lie close to the ancestry of the hyracoids. Superficial resemblances between the Hyracoidea and Notoungulata do occur. There is often some general similarity in the crown pattern of the cheek teeth, and a toxodont curvature of the upper molars is developed for example in the aberrant *Myohyrax* (Pl. 6, fig. 2) ; but the similarity is frequently equalled or exceeded by members of other early groups, such as the Condylarthra or Litopterna, and more particularly the primitive Equoidea. Moreover, there are essential differences in the notoungulate molar, notably the isolated transverse entoconid in the lower teeth, and the

accessory crests developed in the upper teeth. The isolated entoconid, present even in Paleocene notoungulates, seems to be a secondary specialisation, for although absent in early members of the collateral litoptern stock, it is developed in later members of that group. It is unlikely that the typical hyracoid molar, lacking these features, could have been developed from a notoungulate prototype. Again, the brain of notoungulates, as far as can be determined from endocranial casts, appears to have evolved from a condylarthran condition along lines divergent from those found in the Perissodactyla and Artiodactyla (Simpson, 1933 ; Patterson, 1937). The brain of *Procavia*, on the other hand, seems to be of simple, but definitely ungulate type (Elliot Smith, 1902).

The tarsus in both hyracoids and notoungulates is serial, with the astragalus excluded from the cuboid ; and in some notoungulates there is a type of mesaxonic development with broad, shallow astragalar trochlea, resembling that of Hyracoidea, and most Perissodactyla. In other notoungulates, however, there is a tendency towards an artiodactyl or paraxonic symmetry, with a deep, narrow trochlea. In all notoungulates, as in artiodactyls, the fibula articulates with the calcaneum ; and this character becomes increasingly pronounced in late Tertiary notoungulates. A very similar tarsus was developed in another exclusively Neotropical group, the litopterns. In the hyracoids and perissodactyls, the fibula invariably articulates with the astragalus. In hyracoids the astragalar head is almost flat, and the internal malleolus of the tibia fits into a deep, restrictive socket in the side of the astragalus, whereas in notoungulates the astragalar head is semi-circular, and the internal malleolus lies against the side of the astragalus. Finally, the carpus is typically interlocking in notoungulates, and serial in hyracoids.

Similarities and differences between the Notoungulata and Hyracoidea can be summarised as follows :

NOTOUNGULATA	HYRACOIDEA
New World group.	Old World group.
Entoconid isolated and transverse.	Entoconid usually longitudinal, always connected with hypoconid.
Tendency to develop accessory cusps in upper molars.	No marked tendency to develop accessory cusps.
Poorly developed styles in upper molars.	Usually well-developed styles in upper molars.
I ₁₋₂ sometimes forked.	I ₁₋₂ frequently pectinate.
Posterior milk molars resemble molars more than premolars.	Posterior milk molars sometimes resemble molars more than premolars.
Enamel confined to labial face of incisors.	Enamel on all faces of incisors, except in specialised <i>Myohyrax</i> .
Roots present only in deciduous molars.	Roots present in all cheek teeth.
Clavicle sometimes present.	Clavicle probably always absent.
Alternating carpus.	Serial carpus.
Femur with third trochanter.	Femur with third trochanter.
Fibula articulates with calcaneum.	Fibula articulates with astragalus.

NOTOUNGULATA

Internal malleolus of tibia laid against astragalus.
 Serial tarsus, some with mesaxonic, some with paraxonic trend.
 Semi-circular astragalar head.
 Astragalus excluded from cuboid.
 Brain of advanced condylarthran type, modified along characteristic lines.
 No canal penetrating anterior edge of ascending ramus.
 Articular condyle of mandible circular, glenoid broad and shallow.

 Malar does not enter into glenoid.
 Parietal not incorporated in post-orbital process.
 Cancellous dilation of mastoid.
 Palate concave.

HYRACOIDEA

Internal malleolus fits into deep socket in astragalus.
 Serial tarsus, always mesaxonic to some extent.
 Flattened astragalar head.
 Astragalus excluded from cuboid.
 Brain of ungulate type.

 Canal penetrating anterior edge of ascending ramus.
 Articular condyle usually expanded transversely, glenoid narrow. Condyle longitudinally expanded in *Myohyrax*.
 Malar contributes to glenoid.
 Parietal contributes to post-orbital process.
 Cancellous dilation of mastoid.
 Palate concave in some species

The items in this list clearly show the essential difference of these two orders. If further confirmation is needed, it is supplied by the simultaneous acme of hyracoid and notoungulate radiation in Oligocene times, at the close of a long period of marine transgression and continental isolation. The chronological distribution of notoungulate families is Eocene 8, Oligocene 9, Miocene 5, Pliocene 4, and Pleistocene 3; the distribution of hyracoid genera is Oligocene 6, Miocene 5, Pliocene 1 and Pleistocene 1.

If a closer relationship is sought among other groups of mammals, attention is inevitably focused upon the true ungulates, in particular upon the perissodactyls. Schlosser (1911) noted the general similarity existing between the skulls of Oligocene hyracoids and primitive ungulates, and there can be no doubt that a number of fundamental resemblances link the hyracoids with the ungulates. For example, the brain of *Procavia*, particularly in the pattern of the cerebral sulci, is of a simplified but distinctly ungulate type. Wislocki (1930) also suggested that the placenta in *Hyrax* is of a type which may perhaps be regarded as primitive in Ungulata, although T. H. Huxley and others have denied the ungulate affinities of the hyracoid placenta. Again, Murie & Mivart (1865), and Windle & Parsons (1901) repeatedly refer to the ungulate-like musculature of *Hyrax*. In a great number of instances the development of individual muscles in *Hyrax* is very similar to the condition in *Equus*, but occasionally there is an arrangement which is peculiar to these two genera.

In their skeletons, too, hyracoids show a similarity to the ungulate plan, but the resemblance is to the perissodactyl rather than the artiodactyl pattern. The resemblances to certain Perissodactyla are often greater than those existing between the more diverse members of that order. The limbs of hyracoids, wherever known, exhibit a variably mesaxonic arrangement, and the radius always articulates with

two carpals only, as in perissodactyls. The serial carpus, however, is a point of difference: although in the relatively unadvanced tapirs, an intermediate condition, lacking the centrale, is found. The astragalus, as in perissodactyls, possesses a single flattened head, and is not in contact with the cuboid. The fibula engages with the astragalus, whereas in artiodactyls there is a pronounced articulation with the laterally expanded calcaneum. The facetting, relative position and shape of the hyracoid astragalus and calcaneum are also characteristically perissodactyl. In

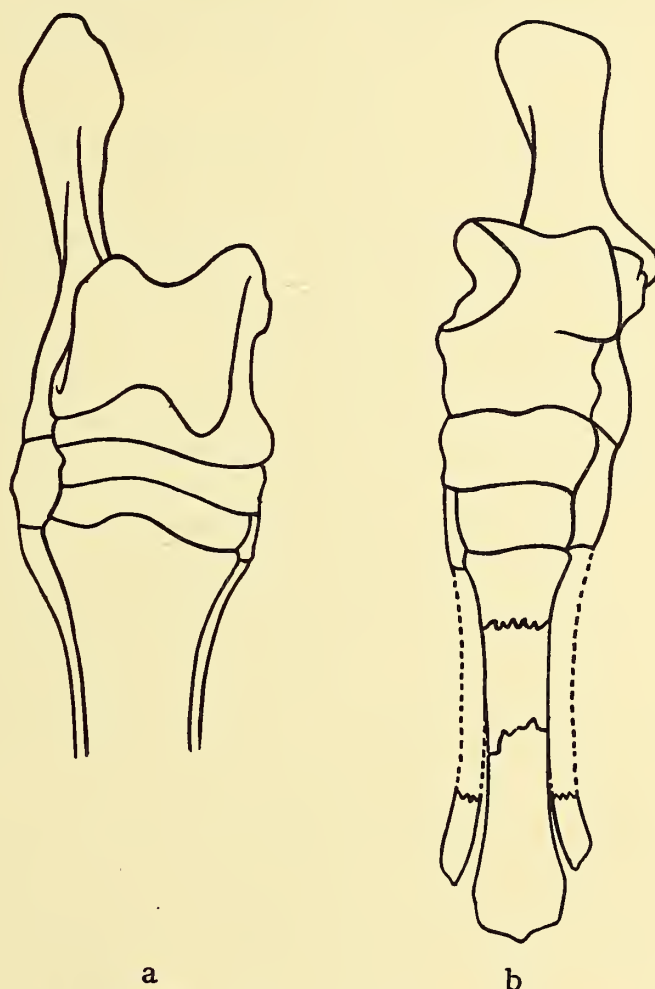


FIG. 17. Dorsal aspect of (a) the tarsus of *Equus caballus*, and (b) the tarsus and metatarsus of *Megalohyrax championi* (334 '47). (a) reduced, (b) natural size.

giant hyracoids of the Oligocene and Miocene, the similarity seems to have reached its extreme expression. The laterally compressed tarsus, and reduced lateral digits of *Megalohyrax championi* show a resemblance to the equid pattern, which exceeds that of other perissodactyls (Text-fig. 17). The variety of mesaxonic structure achieved in the hyracoid tarsus is not dissimilar to that found in Recent perissodactyls. The mesaxonic arrangement is most pronounced in the long-snouted genera, and least in those with short snouts.

In general pattern a hyracoid molar clearly conforms to the bunio-lophodont or lophodont crown of perissodactyl teeth, rather than to the bunoid or selenodont teeth of artiodactyls. The most detailed resemblances to early hyracoid molars are found in the New World horses of the lower Tertiary, or among the palaeotheres of Eurasia. It is most difficult to define more than trivial differences between the molars of early horses and hyracoids, and when the lower jaw of *Pliohyrax graecus* was first described, it was regarded as a palaeothere. Similar mistakes have been made with isolated teeth of *Megalohyrax championi*. On the other hand, more persistent stocks of Hyracoidea, culminating in *Procavia*, progressively develop a molar condition which closely parallels that found in rhinoceroses. It would seem that in the teeth also, Hyracoidea show a divergence roughly equivalent to that occurring within the order Perissodactyla. While none of the resemblances outlined above may be diagnostic in themselves, taken together they are of considerable weight.

It is impossible to arrive at any definite conclusions concerning the immediate ancestry of the Hyracoidea, but certain general possibilities begin to emerge. During the Paleocene, condylarths formed a major part of the American faunas. The molar teeth of two families of condylarths, the Meniscotheriidae and Phenacodontidae, are very like those of early hyracoids and perissodactyls. These condylarthran families are the only ones known to have extended their range into Palaearctica. The condylarths are commonly regarded as the original stock from which all subsequent ungulate or near-ungulate lines arose. Simpson suggested that the hyopsodontid condylarths may have given rise to the Artiodactyla, and some of the phenacodonts to the Perissodactyla. Matthew (1937) took the alternative view, that although known condylarthran groups might have given rise to the extinct American "ungulates", perissodactyls represent a collateral branch of development, at present unknown in the Paleocene, and which arose independently from some remote and extremely primitive creodont stock. Certainly a phenacodont origin of Perissodactyla seems unlikely, if Matthew's earlier contention, that the serial carpus of Phenacodontidae is a secondary feature, is rigidly applied. It is interesting to note, however, that elsewhere in the same monograph, Matthew associated the hyracoids with the perissodactyls, deriving both from similar condylarthran roots.

The suggestion that Phenacodontidae may bear some ancestral relationship to Perissodactyla (and perhaps therefore to Hyracoidea), is not entirely satisfactory. The apparent trend in the carpus of phenacodonts is not easily reconciled with the subsequent development of this joint in either the hyracoids or perissodactyls. Moreover, known phenacodonts are too late to serve in an ancestral role to Perissodactyla, and the same difficulty probably applies equally in the case of the Hyracoidea. In the arrangement of the carpus, meniscotheres present less difficulty, as Matthew (1897) tentatively suggested. In addition, their molar teeth show perhaps the closest similarity of all condylarths to those of early hyracoids. Once again it seems unlikely that known forms can be regarded as ancestral. The meniscotheres are not sufficiently remote in time, and evolved too rapidly in some respects, for there to be any question of direct relationship. In early Eocene times they already exhibit a degree and type of modification in their molar teeth, roughly comparable to that which is later found in hyracoids.

To summarise, the available evidence suggests a development of the Hyracoidea

from some early condylarth-like stock, which may have lain close to the origins of meniscotheres and Perissodactyla. The Eocene is generally regarded as a period of marine transgression over the borders of Africa, severing connection with Palaeartica, and reducing mammalian invasion to a minimum. The hyracoids reached their zenith in Africa during late Eocene to Oligocene times, and their ancestors therefore must have entered the continent in an earlier period. The absence of fossil hyracoids outside Africa before the Pliocene suggests that the pre-hyracoids arrived there at a condylarthran grade of development, and that the emergence of the hyracoids took place in isolation inside Africa.

VI. DISTRIBUTION OF HYRACOIDEA

Although mammal-bearing deposits of Palaeogene age are rare in Africa, the fossil assemblage of the Egyptian Fayum suggests that during the Oligocene, and probably during Eocene times too, a variety of hyracoids was included in the indigenous African fauna. Subsequently their importance seems to have dwindled. In Miocene times they were still widely distributed, but less diverse than in the preceding period. The complete absence of hyracoids from the numerous Miocene sites of southern Europe and the Middle East shows that hyracoids remained confined to Africa at a time when proboscideans, for example, experienced no difficulty in extending their geographic range.

Despite growing land connections during the Miocene and Pliocene, only the ancestors of the apparently localised Pontian *Pliohyrax* seem to have extended their range beyond Africa at this time. Localities where the *Hipparion* fauna has been discovered are numerous, and extend from Spain to Persia, but only Samos and Pikermi have yielded fossil Hyracoidea. This geographical localisation, and the rarity of the hyracoid specimens, would seem to have some real significance. The distribution of *Pliohyrax* might suggest accidental colonisation of a Tethyan island, were it not that the associated fauna shows no other unusual feature. As Forsyth-Major (1891), and Arambourg & Piveteau (1929) have remarked, the characteristic Pontian fauna extends, with only gradual change, over an enormous area. Both the composition and the uniformity of the assemblage suggest continuous plains or plateau conditions throughout its entire range. Apart from the isolated occurrence of *Pliohyrax*, the faunas of Pikermi and Samos readily fit into this general scheme. At present it seems impossible to give any rational explanation of this singular feature of hyracoid dispersal, and one can only say that Samos and southern Greece appear to represent the real distributional limits of *Pliohyrax*.

The ancestors of Pleistocene and Recent hyracoids must have been present in Africa during the Pliocene, but no mammal-containing deposits of undoubted Pliocene age have yet been discovered south of Egypt. Knowledge of Pliocene climate in Africa is mainly conjectural, but, despite evidence of a humid belt along the Nile valley, there is some indication that climatic zones were not dissimilar from those existing today, and that a considerable part of North Africa was occupied by deserts (Moreau, 1952). Thus there is a possibility that within Africa, Pliocene hyracoids were concentrated in the central and southern regions, much as they are today.

The recorded distribution of Pleistocene (Bechuanaland and Transvaal) and Recent hyracoids is represented in Text-fig. 18, but further investigation may show that they are present in many other parts of south and central Africa. Although hyraxes are small, inconspicuous and shy, they are widely distributed and occupy a great variety of habitat, occurring in forests, woodland, savannah, veldt, on plateaux and high mountains. Even in the deserts of North Africa and Arabia, reports



FIG. 18. The recorded distribution of Recent hyracoids.

indicate that hyracoids are to be found in favourable localities. Broadly speaking the Tree Hyrax seems to be confined south of a line from French Guinea to Sokotra, whereas the Bush Coney extends along a North-South belt down the east side of Africa, from Eritrea through the Lakes to the Transvaal. The Rock Hyrax on the other hand, occupies a wider area, including South Africa, the entire eastern side of the continent, parts of the northern deserts, Palestine and Arabia.

VII. EVOLUTIONARY TRENDS IN HYRACOIDEA

Oligocene hyracoids fall readily into two divergent groups, the short-snouted, medium-sized Saghatheria, and the long-snouted, giant Geniohyidae. Whereas the former may represent a more persistent and conservative stock, the latter conform exactly to the accepted pattern of short-lived families, and undergo rapid evolutionary modification coupled with a great increase in size.

The Geniohyidae (*Megalohyrax*, *Geniohyus*, *Bunohyrax* and *Titanohyrax*) seem to have followed a phylogenetic pattern not dissimilar from that suggested by Schlosser (1911: 103). *Geniohyus* and *Bunohyrax* are undoubtedly the most primitive of the Fayûm genera, and it may be that the unspecialised mandible and slightly more

bunoid teeth of the latter approximate closer to the ancestral condition. *Megalohyrax* is distinguished by the possession of less bunoid lower molars, slightly stronger styles in the upper cheek teeth, and more advanced molarisation of the premolars. *Titanohyrax*, which cannot be regarded as other than moderately long-snouted, seems to represent a progressive branch that shows great advance in the cheek teeth along lines initiated in *Megalohyrax*. Of the two primitive forms, the shallow mandible and absence of a mandibular fossa suggest that *Bunohyrax* has closer affinities with *Megalohyrax*. *Geniohyus* and *Bunohyrax* may be regarded provisionally as representatives of two divergent stems, closely related to the ancestral forms, from one of which arose the moderately progressive *Megalohyrax*. *Titanohyrax* no doubt evolved along much the same lines, but modification of the cheek teeth proceeded more rapidly than the elongation of the snout.

The genus *Pachyhyrax* is known by a few isolated teeth, described and figured by Schlosser (1911). These teeth do not support Matsumoto's suggestion that *Pachyhyrax* might be closely associated with *Sagatherium* and *Pliohyrax*. The upper molars in particular are of characteristic geniohyid type, with strongly developed ectoloph and weak transverse crests paralleling the condition found in early Equidae. Although the genus is so imperfectly known, the size and pattern of the upper cheek teeth undoubtedly favour its inclusion within the family Geniohyidae.

Myohyrax clearly represents a widely divergent and aberrant stock. The peculiar features of *Myohyrax*, some highly specialised, others persistently primitive, suggest that it is an ancient offshoot, which departed from the primitive bunoid stem prior to the emergence of the Oligocene genera.

The other Cainozoic hyracoids fall naturally into a second, separate and relatively homogeneous group, universally characterised by a short snout. In many cases, the resemblance between members of this group is very strong. In contrast to the Geniohyidae, this would seem to be a persistent group, showing great stability through a long history. Evolutionary modification of the dentition and skull appears to have been at a minimum during most of Tertiary and Quaternary time. The post-cranial skeleton also, in so far as it is known, seems to have attained to a general hyracoid standard by Oligocene times, and to have suffered very little subsequent change.

Resemblances between *Pliohyrax* and *Procavia* are often most marked. Despite the great difference in size, both have short, broad skulls, with lower jaw of shallow to medium depth. They are the only known hyracoids in which the orbit is ever closed behind. In both genera, the upper external styles are poorly formed (although these are relatively more advanced in *Procavia*), but the development of rhinocerotoid transverse crests in the upper molars is unparalleled in other hyracoids. The compressed, internally-flattened, selenodont and somewhat high-crowned lower cheek teeth are almost identical in pattern. The anterior dentition also corresponds fairly closely, the diastemata in *Procavia* being commensurate with reductions in the full eutherian dentition of *Pliohyrax*. The lower canine of *Pliohyrax*, in contrast to the blade-like tooth of the Geniohyidae, is premolariform; the lower canine of *Procavia* is normally present only as a reduced deciduous tooth.

Despite these similarities, a direct relationship is unlikely. In *Pliohyrax* the third lobe attained its maximum development in the posterior molars of both upper

and lower jaw, and the divergence is further emphasised by the dorsally placed orbit and nares, and the backward displacement of the choanae, which suggest some degree of adaptation to an aquatic habit. It is possible that *Plioxyrax* may have been cut off from the main Ethiopian theatre of hyracoid radiation, and have undergone divergent modification in isolation. Alternatively Greece and Samos may be the farthest extension of an abundant and widespread form, perhaps capable of crossing aquatic barriers, and whose apparent absence from Africa is due to the non-discovery of lower Pliocene deposits there. For the present *Plioxyrax* may be regarded as lying close to, but not directly on the central plexus of procavian evolution.

Saghattherium so closely resembles *Procavia* in the dentition and pattern of the skull, that on purely morphological grounds it must be close to the main ancestral

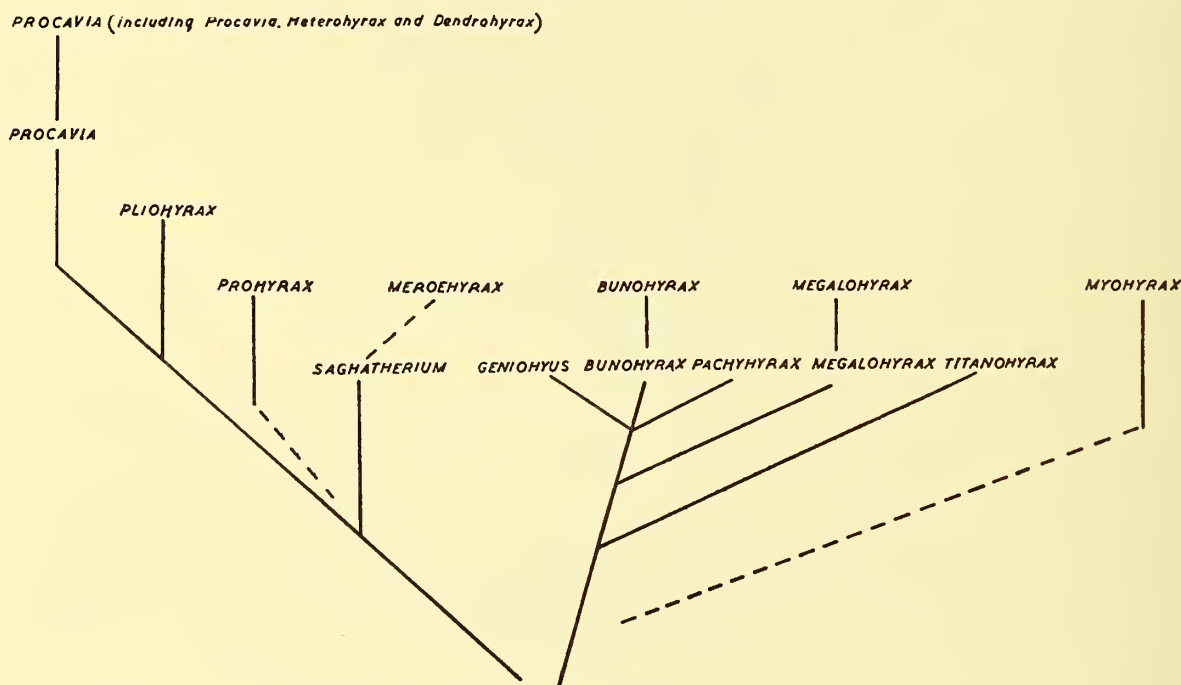


FIG. 19. Diagram showing the suggested relationships of the various hyracoid genera.

stem of modern hyracoids. The presence of a sagittal crest merely reflects the greater size and weight of the skull, which is otherwise exactly similar to that of *Procavia*. The lower cheek teeth of *Saghattherium* are more bunoid than those of *Procavia*, but this is to be expected in a genus so much earlier in time. Despite these similarities, it is doubtful whether there can be any direct relationship between *Saghattherium* and *Procavia*. The former is separated from *Procavia* by an enormous span of time, and shows signs of an evolutionary precocity in its greater size, and in the more advanced development of styles in the upper molars. Hence it seems better to regard *Saghattherium* also as an early offshoot of the main procavian stem.

The close similarities in the dentition of *Saghattherium* and *Meroëhyrax* have been outlined previously. There is reason to think that an intimate relationship may have existed, although material referred to the Miocene genus is insufficient to support

more definite conclusions. The material attributed to Stromer's *Prohyrax tertiarius* is also very sparse. It is obvious, however, that this medium-sized and notably short-snouted form exhibits features in its dentition characteristic of the general procaviid pattern, while differing from other Procaviidae in the extreme forward position of the orbit. For the present, *Prohyrax* must be regarded as a further offshoot of the procaviid or saghatherine stems, progressive along the lines of hypsodonty and styler development.

Text-fig. 19 displays the probable relationships of the various hyracoid genera in diagrammatic form.

VIII. A REVISION OF HYRACOID CLASSIFICATION

It has been demonstrated, in a preceding section, that numerous similarities exist between Hyracoidea and Perissodactyla. Indeed, in certain important respects, some perissodactyls may show a stronger resemblance to hyracoids than to other Perissodactyla. Some of these similarities are clearly examples of adaptive convergence: others, particularly in the earlier genera, suggest a real, and not too remote, affinity. On the other hand, hyracoids share certain characteristics with non-perissodactyl groups, and possess many unique features. Moreover, in some respects they exhibit a diversity comparable to that developed within the order Perissodactyla. For these reasons it is proposed that the hyracoids should be included in the same super-order Mesaxonia Marsh, but should retain an independent ordinal status.

The clear-cut and early division of the hyracoids into two main branches has already been noted. On the balance of evidence it seems unnecessary within the short-snouted group to place *Saghatherium* and *Pliohyrax* in separate families, and all short-snouted genera are here included in the one family Procaviidae. Similarly, the family Geniohyidae should include all long-snouted, giant forms. *Titanohyrax* possesses cheek teeth which differ from those of typical semi-bunoid Geniohyidae in the same manner as those of *Megalohyrax*, but to a greater extent. Indeed, from their dental characters, *Megalohyrax* and *Titanohyrax* might well be referred once again to the same genus. The proportions of the jaws and arrangement of the teeth in *Titanohyrax* also suggest that the snout was fairly long. For these reasons *Titanohyrax* is included within the Geniohyidae, and the family Titanohyracidae discarded.

The peculiar adaptations in the rodent-like *Myohyrax* fully support Andrews' reference of this genus to an independent family. Whether Stromer's sub-order Myohyracoida should also be retained is controversial. For the present, until more complete material is available, it seems better to link Myohyracidae, somewhat loosely, with the Geniohyidae, while recognising that this may be an artificial association. Within the family Myohyracidae certain revisions are necessary. It has been shown (p. 37) that *Myohyrax doederleini* Stromer is a synonym of *M. oswaldi* Andrews. On similar grounds, there seems little reason to separate the two species *Protypotheroides beetzi* Stromer and *M. osborni* Hopwood. All the material described under these names by the two authors should therefore be referred to *M. beetzi* (Stromer).

The long-snouted Geniohyidae differ greatly from the short-snouted Procaviidae.

In addition to their larger size, the former show a progressive development of the cheek teeth along characteristic hippomorphan lines, involving a predominant development of the ectoloph. Broadly speaking the upper premolars of Oligocene Geniohyidae resemble the molar teeth of Eocene horses, their molars those of Oligocene horses. In later or more specialised Geniohyidae, the upper molars are almost indistinguishable from those of early Miocene horses, whereas the premolars resemble the molars of Oligocene or Eocene Equidae. Conversely the Procaviidae show a strong rhinocerotoid development of transverse crests in the upper cheek teeth as early as Pontian times. To a lesser degree this tendency can be found, accompanied however by a fairly strong ectoloph, in the upper molars of lower Miocene Procaviidae; and its beginnings are just discernible in the Oligocene *Sagatherium*. In all forms adequately known, this divergence, closely correlated with the long or short snout, is constant and apparently diagnostic. On this basis, both *Titanohyrax* and *Pachyhyrax* clearly appertain to the Geniohyidae, with the implication that they were relatively long-snouted.

The mesaxonic tarsal pattern of *Megalohyrax championi*, preceded by less distinct but comparable development in Oligocene Geniohyidae, also parallels the advanced hippomorphan condition. The Procaviidae, where known, show a weaker mesaxonic arrangement, with minor reduction of lateral digits almost exactly similar to that found in the less progressive of the Recent Ceratomorpha. Thus there is much the same range of divergence between the relatively impersistent Geniohyidae and more conservative Procaviidae, as separates the perissodactyl sub-orders Hippomorpha and Ceratomorpha. Despite the paucity of hyracoid forms, to bring them into the line with the accepted perissodactyl classification, and to express their variety adequately, it seems necessary to divide the order Hyracoidea into two sub-orders. For these the names Pseudhippomorpha and Procaviamorpha are proposed. The position of Myohyracidae within this scheme is obscured by profound specialisation in their dentition, and an almost complete lack of post-cranial material. For the present it is convenient to associate Myohyracidae provisionally with the Geniohyidae, in the new sub-order Pseudhippomorpha.

On this basis the hyracoids are divided into two sub-orders, the one containing two long-snouted families, the other a single short-snouted family. Although Osborn and Andrews gave separate family status to *Pliohyrax* and to *Sagatherium* and its allies, the divergence between these forms and *Procavia* is appreciably less than between *Myohyrax* and the Geniohyidae. If, therefore, Myohyracidae are only to be separated at family level, then all Procaviamorpha must be included within a single family. The differences between *Procavia*, *Sagatherium* and *Pliohyrax* are better expressed by making each representative of a separate sub-family. The first of these new sub-families, the Sagatheriinae, has already been defined (p. 40). The other two, the Procaviinae and Pliohyracinae, can be defined as follows:

PROCAVIINAE

Small hyracoids with short snout, and permanent dentition reduced to $\frac{1}{2} \frac{0}{0} \frac{4}{3} \frac{3}{3}$.

Upper molars with strong rhinocerotoid development of transverse crests. Posterior third lobe not developed in any of the molar teeth.

PLIOHYRACINAE

Giant hyracoids with short snout, retired choanae and closed, dorsal orbit. Dentition unreduced, upper molars with strong rhinocerotoid development of transverse crests. Posterior third lobe in M^3 and M_{2-3} .

The conclusions outlined above are embodied in the following classification of the Hyracoidea :

Superorder MESAXONIA Marsh, 1884.

Order HYRACOIDEA Huxley, 1869 (incl. Myohyracoida Stromer, 1926)

Suborder PROCAVIAMORPHA

Family PROCAVIIDAE Thomas, 1892 (= Hyracidae Gray, 1821 ;
incl. Pliohyracidae Osborn, 1899 ; in part = Saghatheriidae Andrews,
1906)

Sub-family PROCAVIINAE

Procavia Storr, 1780 (= *Hyrax* Hermann, 1783)

Heterohyrax Gray, 1868

Dendrohyrax Gray, 1868

Sub-family PLIOHYRACINAE (= Pliohyracidae Osborn, 1899)

Plioxyrax Osborn, 1899 (= *Leptodon* Gaudry, 1862, not
Sundevall, 1835)

Sub-family SAGHATHERIINAE (in part = Saghatheriidae Andrews,
1906)

Saghatherium Andrews & Beadnell, 1902

Prohyrax Stromer, 1926

Meroëhyrax gen. nov.

Suborder PSEUDHIPPIOMORPHA

Family GENIOHYIDAE Matsumoto, 1926 (incl. Titanohyracidae Matsumoto, 1926 ; in part = Saghatheriidae Andrews, 1906)

Megalohyrax Andrews, 1903 (= *Mixohyrax* Schlosser, 1911)

Geniohyus Andrews, 1904

Bunohyrax Schlosser, 1911

Pachyhyrax Schlosser, 1911

Titanohyrax Matsumoto, 1921 (= *Megalohyrax* Schlosser,
1911)

Family MYOHYRACIDAE Andrews, 1914

Myohyrax Andrews, 1914 (= *Protypotheroides* Stromer, 1922)

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EXPLANATION OF PLATES

PLATE I

EXPLANATION OF PLATE I

Megalohyrax championi (Arambourg)

Palatal view of skull (M.16387) with C to M³. $\times \frac{3}{4}$.



MEGALOHYRAX

PLATE 2

EXPLANATION OF PLATE 2

Megalohyrax championi (Arambourg)

FIG. 1. Lateral view of skull (M.16387). \times approx. $\frac{3}{4}$.

FIG. 2. Dorsal view of same. \times approx. $\frac{3}{4}$.



2

MEGALOHYRAX

I

PLATE 3

EXPLANATION OF PLATE 3

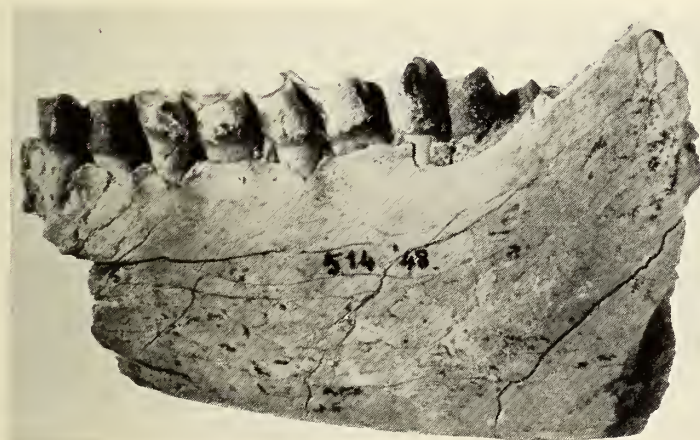
Megalohyrax championi (Arambourg)

- FIG. 1. Lingual view of right mandibular fragment (C.M.Hy.34) with dM_1 to M_2 (M_2 partly erupted), and part of symphysis bearing left I_1 . Approximately natural size.
- FIG. 2. Labial view of left mandibular ramus (C.M.Hy.58) with P_2 to M_3 . \times approx. $\frac{3}{4}$.
- FIG. 3. (a) labial, (b) lingual and (c) occlusal view of left mandibular fragment (514 '48) with P_4 to M_3 . Approximately natural size.
- FIG. 4. (a) labial and (b) occlusal view of left mandibular fragment (C.M.Hy.107) with dM_{2-3} . Approximately natural size.

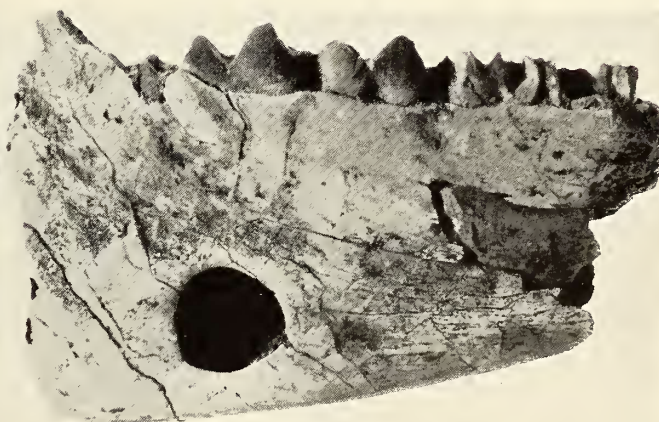
I



2



3a



3b



4a



4b



3c

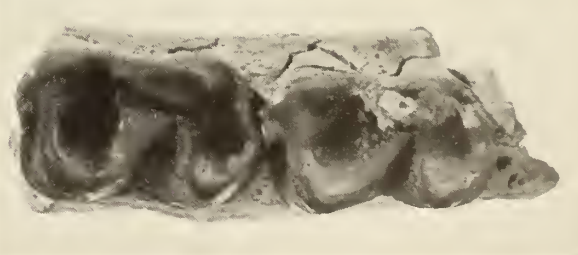
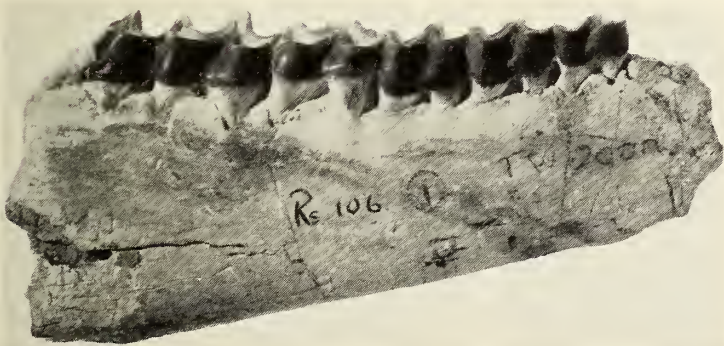
MEGALOHYRAX

PLATE 4

EXPLANATION OF PLATE 4

Megalohyrax championi (Arambourg)

- FIG. 1. Lingual view of right mandibular ramus (C.M.Hy.6) with P_1 to M_3 . \times approx. $\frac{4}{3}$.
- FIG. 2. (a) labial, (b) lingual and (c) occlusal view of right mandibular fragment (C.M.Hy.59) with P_2 to M_2 and anterior lobe of M_3 . Approximately natural size.
- FIG. 3. (a) labial, (b) lingual and (c) occlusal view of right mandibular fragment (C.M.Hy.4) with P_{3-4} . $\times 2$. The teeth in this specimen are almost identical with those of the holotype.



MEGALOHYRAX

PLATE 5

EXPLANATION OF PLATE 5

Megalohyrax championi (Arambourg)

- FIG. 1. Labial view of left maxillary fragment (C.M.Hy.7) with dM^2 to M^2 and P^{2-3} visible within the crypts. Natural size.
- FIG. 2. Labial view of right mandibular fragment (520 '47) with M_2 . This tooth bears an unusually large accessory stylid. $\times 2$.

Myohyrax oswaldi Andrews

- FIG. 3. (a) labial and (b) occlusal view of left maxillary fragment (C.M.Hy.54) with P^4 to M^3 and the anterior portion of the zygomatic arch. \times approx. $4\frac{1}{2}$.
- FIG. 4. (a) labial, (b) lingual and (c) occlusal view of right maxillary fragment (C.M.Hy.55) with P^3 to M^1 . $\times 4\frac{1}{2}$.



1



3a



3b



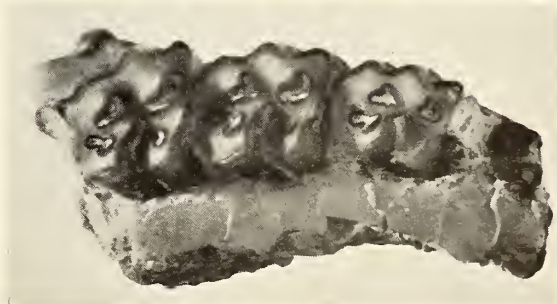
2



4a



4b



4c

MEGALOHYRAX, MYOHYRAX

PLATE 6

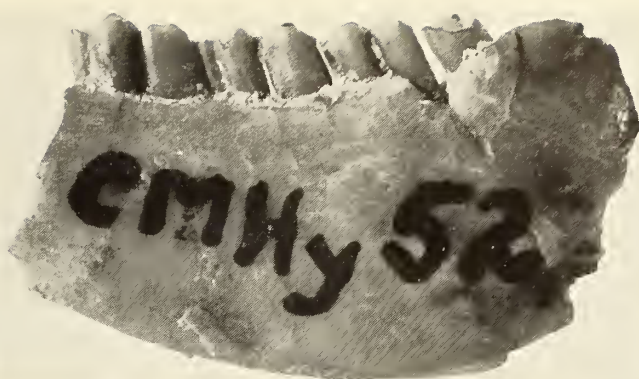
EXPLANATION OF PLATE 6

Myohyrax oswaldi Andrews

- FIG. 1. (a) labial, (b) lingual and (c) occlusal view of right mandibular fragment (C.M.Hy.52) with P₄ to M₃. $\times 5$.
- FIG. 2. Posterior view of the upper molars showing the toxodont curvature of these teeth. Approx. $\times 7$.
- FIG. 3. (a) occlusal, (b) labial and (c) lingual view of left mandibular fragment (C.M.Hy.53) with P₂ to M₃. $\times 4\frac{1}{2}$.



1a



1b



2

1c



3a



3b



3c



MYOHYRAX

PLATE 7

EXPLANATION OF PLATE 7

Meroëhyrax bateae gen. et sp. nov.

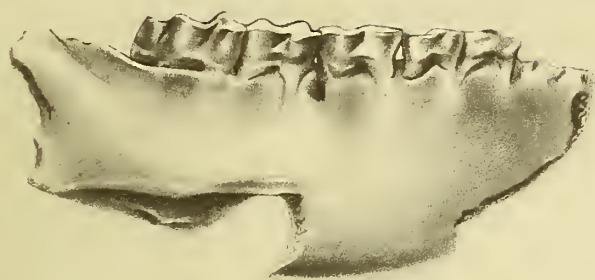
FIG. 1. (a) labial, (b) lingual and (c) occlusal view of the holotype (324 '47), a right mandibular fragment with P₃ to M₃. Natural size.

Megalohyrax sp. (cf. *M. pygmaeus* Matsumoto)

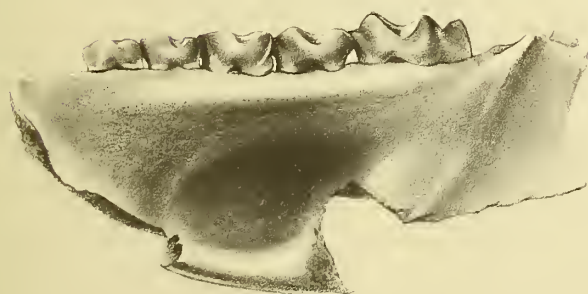
FIG. 2. (a) labial, (b) lingual and (c) occlusal view of right mandibular fragment (C.M.Hy.60) with ?P₄. Natural size.

Bunohyrax sp.

FIG. 3. Occlusal view of isolated upper molar of the left side (Sgr. 311 '48), probably M². Natural size.



1a



1b



1c



2a



2b



2c



3

MEROËHYRAX, MEGALOHYRAX, BUNOHYRAX

PRESENTED

17, MAR 1954



7
340